

THE INFRAGENERIC STRUCTURE OF *VICIA*

F. K. KUPICHA*

ABSTRACT. The genus *Vicia* L. (Leguminosae) has never been treated taxonomically on a world-wide basis. The classification systems used in modern European and Asian revisions are unnatural, because they are based on only a small number of heavily-weighted characters and do not reflect the overall pattern of character-variation within the genus. This paper discusses the variable characters in *Vicia*, emphasising those of greatest taxonomic significance, and presents a new subgeneric and sectional classification. Two subgenera and twenty-two sections are recognised; nine of the latter are described as new.

INTRODUCTION

Vicia is closely related to *Lens* Miller and *Lathyrus* L., so much so that the mutual delimitation of these groups has varied considerably during the taxonomic history of the tribe Viciaeae. Systems of the 18th and 19th centuries, for example, often recognised the genera *Ervum* L., containing members of the modern *Vicia* and *Lens*, and *Orobis* L., comprising species of *Lathyrus* and *Vicia*. The delimitation of the tribe and its genera will be discussed in a future paper. My concept of *Vicia* is the same as that expressed in contemporary Floras, with the exclusion of the monotypic genus *Anatropostylia* (Rech. fil.) Kupicha.

The infrageneric taxonomic structure of *Vicia* has been re-organised many times, chiefly by writers of regional Floras, but virtually never on a world-wide basis. The differences between the systems which have been proposed are due to the selective weighting of a few characters, especially details of the style, the relative lengths of inflorescence and subtending leaf, and the size and colour of flowers. I have tried to achieve a more natural classification by using a wider spectrum of characters, and have extended it to embrace the whole genus.

Contemporary taxonomists dealing with *Vicia* tend to divide this genus into three or four groups whose status varies, according to author, from sectional to subgeneric rank. These groups are '*Cracca*', '*Vicia*', '*Ervum*' and sometimes '*Faba*' (cf. Ball, 1968; Davis & Plitmann, 1970; Radzhi, 1971; Townsend, 1974). I consider, however, that primary divisions of this kind do not give a balanced reflection of broad relationships within the genus. Rather, there appears to be a striking dichotomy of character-states within *Vicia* which can best be expressed in the formation of just two subgenera, *Vicia* (typified by *V. sativa*) and *Vicilla*. The name 'subgenus *Cracca* (Dum.) Gams' cannot be used for the latter, because it is antedated by the subgenera of *Vicia* published by Rouy (1899): *Vicilla*, *Pseudervoidea* and *Ervoidea*. *V. cracca*, the type of sect. *Cracca* Dum., was a member of subgen. *Pseudervoidea*, but as one is free to choose I prefer to use the more euphonious name *Vicilla* for the subgenus. Its type is *V. pisiformis*.

Subgenus *Vicia* is the smaller taxon and can be circumscribed in a more positive way than subgen. *Vicilla*, as its members all have several distinctive

* British Museum (Natural History), Cromwell Road, London SW7 5BD.

features in common. There is also a wealth of taxonomically useful evidence providing differential characters within the subgenus, and its sectional classification is comparatively straightforward. In contrast, the range of variation within subgen. *Vicilla* is very wide so that it is difficult to define, and there is only a small degree of correlation between variation in different characters. This situation presents difficulties for the taxonomist. If he chooses variation in a single part of the plant as a basis for sectional grouping, then the groups are conveniently large but certainly unnatural. If, however, only convincingly natural assemblages of species (i.e. groups which share several traits) are accepted as sections, a too finely divided system is produced. I have tried to keep a balance between these two extremes, but perhaps leaning towards the latter alternative. The perennial species tend to fall into the larger sections, while several of the annuals, whose morphological diversity is more extreme and disjunct, have been placed in monotypic or ditypic sections. The taxonomic structure which is produced has the same general pattern as that of the whole tribe.

Note. Ascherson & Graebner's concept of the taxonomic hierarchy was different from that currently expressed in the *International Code of Botanical Nomenclature*. Although this is not quite clear from the text of their *Synopsis der mitteleuropäischen Flora* (1909), the index shows that taxa of sectional rank were sometimes grouped into higher taxa, also called sections. I have followed the synopsis of their classification by Janchen (1957), and accept the groups *Vicilla*, *Atossa* and *Hypechusa* as currently published sections. The higher taxa into which these were assembled are here referred to as 'sections'. Thus, according to Ascherson & Graebner, *Vicia* comprised four 'sections': *Euvicia*, *Faba*, *Cracca* and *Ervum*; *Euvicia* contained two sections, *Atossa* and *Hypechusa*.

Vicia L., Sp. Pl. 734 (1753).

Perennial and annual herbs with erect or more usually climbing or sprawling habit; plants never tuberous. *Stems* angled but never winged, usually with complete replacement of cortical vascular bundles at the nodes, occasionally with partial replacement. *Leaves* hypostomatic to epistomatic, paripinnate and tendrillous or mucronate or very rarely imparipinnate, usually with several to many pairs of leaflets, very rarely unijugate; stipules semisagittate or simple, sometimes toothed or laciniate, occasionally dimorphic, sometimes with a nectary on abaxial side; vernation of leaflets conduplicate (supervolute in *V. biennis*); venation pinnate, brochidodrome. *Inflorescence* racemose, 1-many-flowered, occasionally branched. *Calyx* usually with oblique mouth and teeth of unequal length ('irregular'), sometimes actinomorphic ('regular'). *Vexillum* oblong, stenonychioid or platonychioid, very rarely bossed or pouched at the fold, rarely pubescent on inner face. *Alae* usually with 'pleat' in upper edge of limb. *Staminal tube* oblique at apex. *Style* linear, not contorted, dorsally or laterally compressed or occasionally terete, always hairy; distribution of pubescence various but style never hairy on adaxial side only (except in some specimens of *V. ervilia*). *Legume* compressed or occasionally subtorulose, often stipitate, sometimes hairy but hairs rarely tuberculate; pod sometimes containing 'woolly' parenchymatous tissue between the seeds. *Seeds* with short to long hilum;

testa smooth or very rarely rough; lens near hilum or occasionally on opposite side of seed; free amino acid canavanine sometimes present.

Type: *V. sativa* L.

Members of *Vicia* are distributed throughout temperate regions of the northern hemisphere and in temperate S America. The genus, which comprises about 140 species, has its main centre of diversity in the Mediterranean (Tethyan) area with smaller centres in N and S America.

TAXONOMIC CHARACTERS

The characters discussed here were selected *a posteriori* from the large number of variable traits within *Vicia*. Their patterns of variation were found to be of particular taxonomic significance, and they form the basis of the present classification. The residue of variable characters is mentioned more briefly at the end of this section. These secondary features, which vary more or less independently of each other and of the main characters, tend to supply the differences between closely related species.

CAULINE VASCULAR ANATOMY. Members of sect. *Hypechusa* are distinguished from the rest of the genus by having a modified type of nodal vasculature (Kupicha, 1975).

STIPULES. All members of subgen. *Vicia* possess a more or less conspicuous nectariferous spot on the abaxial face of each stipule. This character, among others, was used by Alefeld (1861) as the basis for dividing his tribe Viciidae (equivalent to *Vicia*) into subtribes Viciosae (with nectaries) and Ervosae (without). Illustrations of the appearance and anatomy of the stipular nectary in *V. sepium* are given by Gams (1924). A transverse section of the stipule shows that the surface of the nectary is sunk below the level of the epidermis, and the floor of this shallow pit is densely covered with a mixture of simple and glandular hairs. According to the figure in Guinea (1953), *V. ervilia* also has stipular nectaries, and the illustration is reproduced by Hermann (1960). Gunn (1969) actually states that this character is present. I have not found nectaries of this type in *V. ervilia* or in any other species outside subgen. *Vicia*, but confirm that they occur in every member of this group. The role of the extrafloral nectaries is discussed on page 293.

EPIDERMAL STRUCTURE OF LEAVES. The first investigation into the epidermal structure of the Viciae was reported in 1902 by Streicher, who described the shape of the epidermal cells and the distribution of stomata, hairs, sclerenchyma and cell inclusions in several species of each genus. His work led him to conclude that these characters have little importance in the taxonomy of the group, and they have since been largely ignored except in *Lathyrus*, where variation in epidermal characters has recently been more fully explored and exploited by Bässler (1966) and Simola (1968). My own investigations in *Vicia* parallel the work of Simola in *Lathyrus*; like her, I use the Stomatal Index formula, devised by Salisbury (1928), to describe the relative proportions of stomata and other epidermal cells on the leaf surface.

$$\text{Stomatal Index} = \frac{\text{No. of stomata per unit area}}{\text{Total no. of epidermal cells in the same area}} \times 100$$

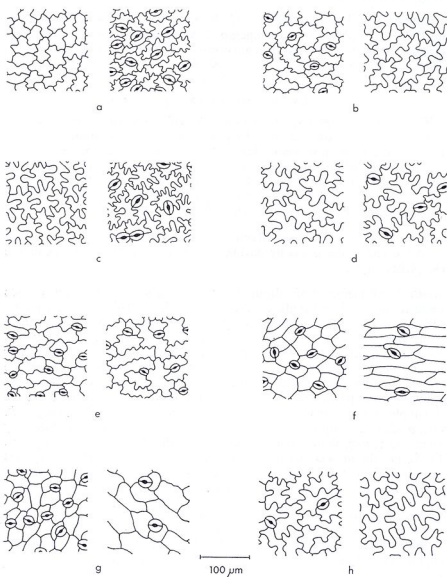


FIG. 1. The upper (left) and lower (right) leaf epidermis in species of *Vicia*: a, *V. unijuga*; b, *V. orobus*; c, *V. oroboides*; d, *V. truncatula*; e, *V. villosa*; f, *V. filicaulis*; g, *V. pulchella*; h, *V. nigricans*.

Salisbury showed, by a long and detailed series of experiments on British woodland plants, that "the increased stomatal frequencies in plants grown on dry soil as compared to those grown on wet soil, and of small leaves as compared to large leaves, are . . . due chiefly to differences in the spacing of stomata and not to differences in the proportion of stomata developed. This appears to be true also for the variations in frequency in different parts of the same leaf."

Materials and methods. The structure of the epidermis was determined from fully-grown leaflets, one specimen from each species being examined. Some material was fresh, while leaves from herbarium specimens were prepared by soaking in 5% KOH at room temperature for one to three days. Using a fine pair of forceps, pieces of epidermis were stripped off the leaflet and mounted in glycerine jelly. The appearance of most epidermides was then recorded by drawing them, using a camera lucida; a selection of these is reproduced in figure 1. The epidermal cells were counted in five fields of view, totalling an area of 0.23 mm². Although this is less than one-third the area used by Simola in her calculations, I obtained results very similar to hers (in my study of *Lathyrus*) and therefore have assumed that the method is sufficiently accurate, especially as only approximate results are necessary. From these scores the Stomatal Index for the upper and lower epidermis of leaves of each species was calculated, and then the latter divided into the former to express in a single number the relative distribution of stomata on both sides; a result near zero indicates a strongly hypostomatic leaf, while a high result is given by an epistomatic leaf. The Stomatal Index Ratios for *Vicia* are shown in Table 1.

TABLE 1. Stomatal Index Ratios in *Vicia*

subgenus VICILLA

Sect. Vicilla		Sect. Cracca	
<i>V. unijuga</i>	0.0	<i>V. cracca</i>	3.3
<i>V. crocea</i>	0.2	<i>V. pinetorum</i>	1.7
<i>V. venosa</i>	0.0	<i>V. ochroleuca</i>	2.7
<i>V. kulingiana</i>	0.0	<i>V. glareosa</i>	1.2
<i>V. pseudo-orobus</i>	0.0	<i>V. sicula</i>	1.2
<i>V. venulosa</i>	0.9	<i>V. alpestris</i>	0.8
<i>V. dichroantha</i>	0.4	<i>V. rafigae</i>	1.2
<i>V. amoena</i>	0.8	<i>V. glauca</i>	1.8
<i>V. amurensis</i>	0.6	<i>V. villosa</i>	1.1
<i>V. sylvatica</i>	1.9	<i>V. benghalensis</i>	1.3
		<i>V. filicaulis</i>	1.3
		<i>V. monantha</i>	1.5
		<i>V. leucantha</i>	2.8
		<i>V. palaestina</i>	1.6
		<i>V. disperma</i>	1.5
		<i>V. vicioides</i>	1.1
		<i>V. hirsuta</i>	3.8
		<i>V. acutifolia</i>	1.7
		<i>V. caroliniana</i>	2.1
		<i>V. exigua</i>	1.3
		<i>V. hugeri</i>	6.9
		<i>V. ludoviciana</i>	1.5
		<i>V. mexicana</i>	∞
		<i>V. pulchella</i>	1.6
Sect. Cassubicae			
<i>V. dadianorum</i>	∞		
<i>V. abbreviata</i>	∞		
<i>V. orobus</i>	∞		
<i>V. sparsiflora</i>	3.5		
<i>V. multicaulis</i>	3.8		
<i>V. semiglabra</i>	3.9		
<i>V. nigricans</i>	∞		
Sect. Perditae			
<i>V. dennesiana</i>	∞		

Sect. Variegatae		Sect. Ervoideis	
<i>V. canescens</i>	1.0	<i>V. articulata</i>	1.5
<i>V. megalotropis</i>	∞		
Sect. Pedunculatae		Sect. Ervilia	
<i>V. altissima</i>	1.3	<i>V. ervilia</i>	1.3
<i>V. onobrychioides</i>	3.9	(<i>V. quadrifuga</i>)	1.0
Sect. Americanae		Sect. Lentopsis	
<i>V. americana</i>	1.3	<i>V. caesarea</i>	1.0
Sect. Subvillosae		Sect. Trigonellopsis	
<i>V. subvillosa</i>	1.0	<i>V. cypria</i>	3.3
Sect. Volutae		<i>V. lunata</i>	4.4
<i>V. biennis</i>	1.3	Sect. Australes	
Sect. Panduratae		<i>V. bijuga</i>	1.4
<i>V. cassia</i>	1.1	<i>V. graminea</i>	1.3
Sect. Ervum		<i>V. nana</i>	1.1
<i>V. pubescens</i>	∞	Sect. Mediocinctae	
<i>V. tetrasperma</i>	2.2	<i>V. leucophaea</i>	2.5

subgenus VICIA

Sect. Atossa		Sect. Hypechusa	
<i>V. oroboides</i>	0.0	<i>V. galeata</i>	0.7
<i>V. balansae</i>	0.0	<i>V. melanops</i>	0.9
<i>V. sepium</i>	0.0	<i>V. noeana</i>	0.9
<i>V. truncatula</i>	0.5	<i>V. pannonica</i>	0.9
Sect. Vicia		<i>V. assyriaca</i>	1.0
<i>V. pyrenaica</i>	0.9	<i>V. hyrcanica</i>	1.0
<i>V. sativa</i>	0.4	<i>V. hybrida</i>	1.3
<i>V. grandiflora</i>	0.5	<i>V. anatolica</i>	1.3
<i>V. cuspidata</i>	0.7	<i>V. lutea</i>	1.6
Sect. Faba		Sect. Peregrinae	
<i>V. faba</i>	0.8	<i>V. michauxii</i>	1.0
<i>V. narbonensis</i>	0.7	<i>V. peregrina</i>	1.0
<i>V. bithynica</i>	0.9		

Results. It is evident that the variation in stomatal distribution is not random. The majority of species have amphistomatic leaves, but certain groups are either hypo- or epistomatic. While these results have proved very useful for taxonomy, it is difficult to interpret them ecologically. Broadly speaking, amphistomatic species live in open habitats; this category includes the annuals, many of which are weeds, and perennials colonising scree and rocky pastures (e.g. *V. pyrenaica*, *V. rafigae*). On the other hand, the strongly epistomatic and hypostomatic types (members of sections *Cassubicae*, *Perditae*, *Vicilla* and *Atossa*) are nearly all woodland plants.

INFLORESCENCE. In *Vicia* the inflorescence is basically racemose. Usually a simple scape arises from the axil of a foliage leaf and bears several to many flowers which are spirally arranged but secund. A few E Asian perennials,

all members of sect. *Vicilla* (e.g. *V. kulingiana*, *V. pseudo-orobus*, *V. unijuga*, *V. venosa* and *V. nipponica*), have compound racemes (i.e. panicles) in which reduced, bractiform leaves subtend each branch of the inflorescence. Bracteoles are rare in the genus, again being confined to sect. *Vicilla*.

Most perennials have dense, many-flowered racemes; exceptions include *V. pyrenaica*, *V. subvillosa* and the American *V. bijuga* and *V. americana*. Annuals usually have inflorescences with 1-5 flowers, except for some members of sect. *Cracca*, e.g. *V. villosa* and *V. benghalensis*.

Peduncle length is a significant and useful character: in members of subgen. *Vicilla* the scape is almost always equal to or longer than the subtending leaf, while in subgen. *Vicia* the peduncles are very short or absent. All members of subgen. *Vicia* also possess stipular nectaries, and it seems likely that these traits are linked functionally. It may be that insects which are attracted to the stipules, being automatically brought close to the flowers, may then effect pollination (Plitmann, 1967); on the other hand, Proctor & Yeo (1973) consider the stipular nectaries to be decoys which distract undesirable visitors from the flowers. I have seen ants on the stipules of *V. sativa* and *V. faba*, and they are shown by Gams (1924) on *V. sepium*. Knuth (1908) says that these ants protect the plants against caterpillars. According to Manley (1948), *Apis mellifera* gathers 'honey-dew' from the stipular nectaries of vetches, and this source can make a significant contribution towards the honey-yield of a hive, although it is considered to produce a poor quality honey.

V. bithynica (sect. *Faba*) is anomalous in having peduncles and pedicels of very variable length; sometimes the flower is sessile, while in other specimens, or at other nodes of the same plant, it is borne on a stem as long as the leaf. There does not seem to be any pattern underlying this variation. Members of sect. *Atossa* have short, close-flowered inflorescences, as do *V. pannonica* and *V. melanops* (sect. *Hypechusa*). Members of sect. *Vicia*, and most of sect. *Hypechusa*, have one or two sessile flowers per node. In sect. *Peregrinae* the solitary flower is borne on a relatively long pedicel, but the peduncle is absent.

Within *Vicia* there appears to be a trend towards greater simplicity in the inflorescence: from panicles to racemes, from bracteolate to ebracteolate pedicels, from many to few flowers, from long to short peduncles. The trend is 'read' in this direction because complex inflorescences tend to occur in species which are thought to be primitive in other characters, while simple inflorescences are found in relatively advanced species.

THE FLOWER. The general floral structure in *Vicia* may be illustrated by taking one species—*V. cracca*—and describing its flower in detail (fig. 2). The androecial characters are constant within the genus but the other parts are variable, providing important taxonomic information.

V. cracca. The calyx is gamosepalous, with unequal free lobes of which the uppermost two are the shortest. The petals are intricately shaped, and fit together in a precise manner by which the flower forms a unit with a mechanism well adapted to pollination by bees. The lower edges of the two keel petals are fused from their apex to half-way along the claw. The anthers are clustered round the end of the style, and are held closely in this position within the apex of the carina. The upper edges of the keel petals are free, and

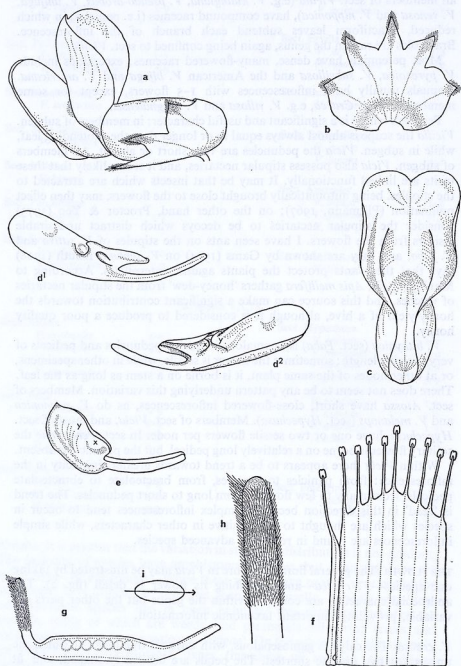


FIG. 2. *Vicia cracca*: a, flower; b, calyx; c, standard; d, wing (d¹ outside, d² inside); e, keel (process 'x' of wing is adnate to hollow 'x' of keel, pleat 'y' of wing rests on keel at 'y'); f, androecium; g, ovary; h, detail of style; i, diagrammatic transection of style with arrow pointing to base of ovary. a-e $\times 5$; f $\times 7$; g $\times 10$; h $\times 25$.

on each side there is a long groove. The alae correspond in shape with the carina; each wing has a thumb-like process ('x' in fig. 2d²) whose papillate lower surface is clearly united with the keel at 'x', while the upper part of the wing is pleated to form a shelf 'y' which rests upon the upper part of the carina at 'y'. The standard turns back sharply from the wings, while its lower part grasps the claws of the keel and wings firmly in place round the staminal tube. The androecium is basically diadelphous; the filament of the uppermost (vexillary) stamen is lightly adnate to the staminal tube formed by the other nine. At the base, however, it is free and raised up, leaving an opening on each side. Nectar, produced abundantly at the base of the ovary, exudes from these pores. The staminal tube ends obliquely. The stamens are alternately long and short, the shortest being the vexillary stamen and the longest the abaxial one. The anthers are introrse, of uniform size and all versatile. The ovary is linear and compressed laterally. The style is also laterally compressed and is hairy all round, with slightly longer hairs on the abaxial side at the apex. The stigma is terminal. The flower is slightly protandrous; pollen escapes from the bursting anthers into the pouched apex of the keel, and collects in a mass round the stigma. The hairs on the style help to brush the pollen up into this position, where it is ready to be transferred to a bee or other insect visiting the flower for nectar.

Calyx. In *Vicia* the free lobes of the calyx are shorter than, or equal to, the tube; they are almost always unequal in length, the abaxial one being the longest. The exceptions with a regular calyx include members of sects. *Vicia*, *Faba*, *Subvillosae*, *Ervoidea* and *Ervillea*, some of sect. *Ervum*, the smallest-flowered species in sect. *Cracca* (e.g. *V. vicioides* and *V. hirsuta*) and *V. cappadocica* (sect. *Panduratae*). *V. caesarea* is unusual in having the upper calyx lobes longer than the abaxial one. The irregular calyx, while typical of most members of *Vicia*, is particularly pronounced in some species of sect. *Cracca* (e.g. *V. cracca*, *V. villosa* and *V. benghalensis*); here the calyx is moderately to strongly gibbous at the base on the adaxial side.

Corolla. Except for using isolated 'spot' characters, e.g. the presence of pubescent standards in some members of sect. *Hypechusa*, taxonomists have paid little attention to the petals of *Vicia*, but having made a detailed survey of flowers in the genus I found considerable variation in the corolla. The shape of the standard varies appreciably, and three main forms can be distinguished (the terms used for the different shapes are taken from Davis 1970, p. 51):

■ Oblong: the banner and claw are approximately equal in width and are not, or scarcely, separated by a 'waist' (fig. 3a, b & i).

Platonychoid or pandurate: the banner and claw are equal in width but are separated by a pronounced 'waist'; the standard is usually deeply cleft at the apex (fig. 3c & d).

Stenonychoid or obovate-spathulate: the banner is wider than the claw (fig. 3e-h, j-l).

These three types are not always well defined, but their distribution is of taxonomic interest, as can be seen from Table 2. The platonychoid vexillum characterises three sections: *Cracca*, *Variegatae* and *Panduratae*; in each case it is associated with a different kind of style. The oblong standard occurs

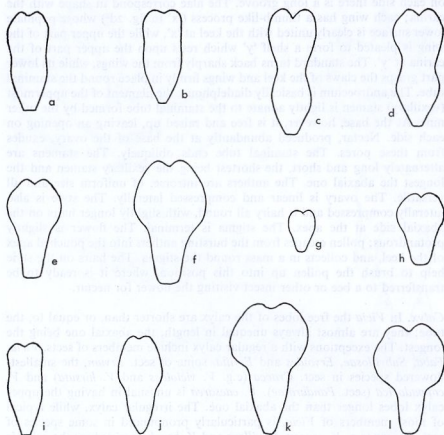


FIG. 3. Vexillum shapes in *Vicia*: a, *V. crocea*; b, *V. abbreviata*; c, *V. alpestris*; d, *V. canescens*; e, *V. onobrychioides*; f, *V. subvillosa*; g, *V. ervilia*; h, *V. cypria*; i, *V. truncatula*; j, *V. narbonensis*; k, *V. galeata*; l, *V. sativa*. All $\times 1\frac{1}{3}$.

predominantly in perennial species with many-flowered racemes. Species with stenonychioid vexilla tend to be those with few-flowered racemes, where the individual flower, rather than the inflorescence, is the attractive unit.

In most members of *Vicia* the standard is marked by two strong fold lines where it recurves from the wings, but in *V. sylvatica* this petal turns back quite smoothly. *V. caesarea* is unusual in having a pair of small shallow pouches on the vexillum at this point.

Most members of *Vicia* have wing petals similar to those of *V. cracca* (fig. 2d), but in a few the pleat which forms the upper process is absent: *V. sylvatica*, *V. tetrasperma*, *V. articulata*, *V. ervilia*, *V. caesarea*, *V. cuspidata* and *V. bithynica*. These species obviously do not form a homogeneous taxonomic assemblage, and it seems that this trait may have arisen several times by simplification of the wing shape. In some of the small-flowered annuals the simpler type of wing may be correlated with autogamy, since the flower is here no longer required to function as a mechanism in insect pollination.

TABLE 2. Vexillum shape and styler types in *Vicia*

		subgenus VICILLA			
	vexillum	style		vexillum	style
Sect. Vicilla			Sect. Pedunculatae		
<i>V. crocea</i>	A	○	<i>V. altissima</i>	C	■
<i>V. kulingiana</i>	A	□	<i>V. cedretorum</i>	C	■
<i>V. pseudo-orobus</i>	A	□	<i>V. onobrychioides</i>	C	■
<i>V. dichroantha</i>	A	□			
<i>V. amoena</i>	A	□	Sect. Americanae		
<i>V. amurensis</i>	A	□	<i>V. americana</i>	A	■
<i>V. pisiformis</i>	A	□			
<i>V. sylvatica</i>	A	□	Sect. Subvillosae		
<i>V. dumetorum</i>	A	■	<i>V. subvillosa</i>	C	□*
Sect. Cassubicae			Sect. Volutae		
<i>V. cassubica</i>	A	□	<i>V. biennis</i>	C	□
<i>V. dadianorum</i>	A	□			
<i>V. abbreviata</i>	A	□	Sect. Panduratae		
<i>V. orobus</i>	A	□	<i>V. cappadocica</i>	B	■
<i>V. multicaulis</i>	A	□	<i>V. cassia</i>	B	■
<i>V. nigricans</i>	A	□	<i>V. cretica</i>	B	■
Sect. Perditae					
<i>V. dennesiana</i>	A	△	Sect. Ervum		
Sect. Cracca			<i>V. laxiflora</i>	C	□
<i>V. cracca</i>	B	△	<i>V. pubescens</i>	A	○
<i>V. pinetorum</i>	B	△	<i>V. tetrasperma</i>	C	□
<i>V. sibthorpii</i>	B	△			
<i>V. ochroleuca</i>	B	△	Sect. Ervoidea		
<i>V. alpestris</i>	B	△	<i>V. articulata</i>	A	□
<i>V. sicula</i>	B	△			
<i>V. ciceroides</i>	B	△*	Sect. Ervilia		
<i>V. rafageae</i>	B	△*	<i>V. ervilia</i>	C	□*
<i>V. multijuga</i>	B	△*			
<i>V. glauca</i>	B	△	Sect. Lentopsis		
<i>V. villosa</i>	B	△	<i>V. caesarea</i>	C	□
<i>V. benghalensis</i>	B	△			
<i>V. scandens</i>	B	△	Sect. Trigonellopsis		
<i>V. cirrhosa</i>	B	△	<i>V. cypria</i>	C	□
<i>V. chaetocalyx</i>	B	△	<i>V. lunata</i>	C	□
<i>V. filicaulis</i>	B	△	<i>V. singarensis</i>	C	□
<i>V. monantha</i>	B	△			
<i>V. leucantha</i>	B	△	Sect. Australes		
<i>V. palaestina</i>	B	△	<i>V. andicola</i>	A	■
<i>V. disperma</i>	B	△	<i>V. bijuga</i>	C	■
<i>V. durandii</i>	B	△	<i>V. graminea</i>	C	■
<i>V. vicioides</i>	B	○	<i>V. linearifolia</i>	C	■
<i>V. hirsuta</i>	C	○	<i>V. nana</i>	C	■
<i>V. acutifolia</i>	B	△			
<i>V. caroliniana</i>	B	△	Sect. Mediocinctae		
<i>V. exigua</i>	B	△	<i>V. leucophaea</i>	C	○*
<i>V. ludoviciana</i>	B	△			
Sect. Variegatae					
<i>V. argentea</i>	B	■*			
<i>V. canescens</i>	B	■*			
<i>V. megalotropis</i>	B	■*			

subgenus VICIA

	vexillum	style		vexillum	style
Sect. Atossa			Sect. Hypechusa		
<i>V. oroboides</i>	A	■	<i>V. anatolica</i>	A	■
<i>V. sepium</i>	A	■	<i>V. assyriaca</i>	C	■
<i>V. balansae</i>	A	■	<i>V. galeata</i>	C	■
<i>V. truncatula</i>	A	■	<i>V. hybrida</i>	C	■
Sect. Vicia			<i>V. hyrcanica</i>	C	■
<i>V. sativa</i>	C	■	<i>V. lutea</i>	C	■
<i>V. grandiflora</i>	C	■	<i>V. melanops</i>	A	■
<i>V. lathyroides</i>	C	■	<i>V. noeana</i>	C	■
<i>V. cuspidata</i>	C	■	<i>V. pannonica</i>	A	■
Sect. Faba			<i>V. sericocarpa</i>	C	■
<i>V. faba</i>	C	■	Sect. Peregrinae		
<i>V. narbonensis</i>	C	■	<i>V. michauxii</i>	C	■
<i>V. bithynica</i>	C	■	<i>V. peregrina</i>	C	■

Vexillum shape: A, oblong; B, platonychoid; C, stenonychoid.

Stylar type: ○, style terete; □, style dorsally compressed, evenly pubescent; ■, style dorsally compressed, tufted abaxially; △, style laterally compressed; *, indicates a distinct variation, as described in text and illustrated in figure 4.

The shape of the keel varies in relation to the wings. I have not observed any strikingly characteristic type except that in subgen. *Vicia* the apical part, containing the style and anthers, tends to be more pouched than in subgen. *Vicilla*, the fused edge curving round above the style.

Gynoeceum. Characters derived from the gynoeceum have traditionally held a prominent place in the taxonomy of the Viciae, as the genera themselves can be distinguished largely on the shape of the style and the distribution of indumentum on it. During this century, stylar characters within *Vicia* have been rather neglected and sometimes loosely or wrongly described, although in the recent classification of Radzhi (1971) and in Townsend (1974) they again receive special attention. A binocular dissecting microscope was used for all the observations recorded here, which were made on both living and herbarium material.

All members of *Vicia* have pubescent styles, although in the smallest-flowered annuals they may superficially appear glabrous due to their size. In most species the style is compressed, either dorsally or laterally (see Table 2).

Members of sect *Cracca* are characterised by a laterally compressed style; it is usually evenly pubescent all round or slightly tufted abaxially (fig. 2g, h), but in *V. ciceroides*, *V. multijuga* and *V. rafigae* (fig. 4c) the two flat sides of the style facing laterally are free from hairs. The only other species known to have a laterally compressed style is the probably extinct *V. dennesiana* (sect. *Perditae*); here again the style is evenly pubescent.

Among the dorsally compressed styles is found a much wider range of indumentum-distribution types. Members of sects. *Vicilla* (except *V. dumetorum*), *Cassubicae*, *Volutae*, *Ervum*, *Ervoides*, *Lentopsis* and *Trigonelopsis* have evenly hairy styles. Subgenus *Vicia* is characterised by styles which are tufted on the abaxial side (the adaxial face have may a few short

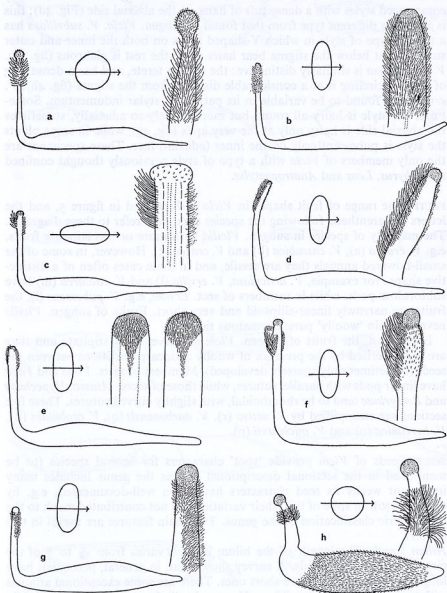


FIG. 4. Variations in styler shape and indumentum in *Vicia*: a, *V. crocea*; b, *V. nigricans*; c, *V. rafifgae*; d, *V. argentea*; e, *V. subvillosa*; f, *V. americana*; g, *V. ervilia*; h, *V. leucophaea*. The elliptic symbols are diagrammatic transections of each style with arrow pointing to base of ovary. Not to scale.

hairs). This kind of style is found also in some members of subgen. *Vicilla*: sects. *Pedunculatae*, *Panduratae*, *Americanae* (fig. 4f), *Australes* and *V. dumetorum* (sect. *Vicilla*). Members of sect. *Variegatae* have dorsally compressed styles with a dense tuft of hairs on the abaxial side (Fig. 4d); this is a slightly different type from that found in subgen. *Vicia*. *V. subvillosa* has a unique type of style in which V-shaped areas on both the inner and outer surfaces just below the stigma bear hairs while the rest is glabrous (fig. 4e). *V. leucophaea* is similarly distinctive: the style is terete, and has a dense ring of hairs encircling it at a considerable distance from the stigma (fig. 4h). *V. ervilia* was found to be variable in its pattern of stylar indumentum. Sometimes the style is hairy all round but more densely so adaxially, sometimes the abaxial side is hairy only at the very apex (fig. 4g), while in some plants the style is pubescent only on the inner (adaxial) face. These specimens are the only members of *Vicia* with a type of style previously thought confined to *Lathyrus*, *Lens* and *Anatropostylia*.

FRUIT. The range of fruit shapes in *Vicia* is illustrated in figure 5, and the letters in parenthesis following the species cited here refer to these diagrams. The majority of species in subgen. *Vicilla* have more or less stipitate fruits, e.g. *V. crocea* (a), *V. cassubica* (b) and *V. cracca* (c). However, in some of the small-flowered annuals they are sessile, and in these cases often of a distinctive shape: for example, *V. articulata*, *V. ervilia* (l) and *V. caesarea* (m) have subtorulose pods, while in members of sect. *Ervum*, e.g. *V. pubescens* (i), the fruits are narrowly linear-ellipsoid and very short. Fruits of subgen. *Vicilla* never contain 'woolly' parenchymatous tissue.

In contrast, the fruits of subgen. *Vicia* are never truly stipitate and they are characterised by the presence of woolly endocarp partitions between the seeds (sometimes only sparsely developed). Members of sects. *Vicia* and *Faba* have linear pods with parallel sutures, while those of sects. *Atossa*, *Hypechusa* and *Peregrinae* tend to be rhomboidal, with slightly curved sutures. These five sections are exemplified by *V. sativa* (r), *V. narbonensis* (q), *V. oroboides* (n), *V. hyrcanica* (o) and *V. michauxii* (p).

SEEDS. Seeds of *Vicia* provide 'spot' characters for several species (to be mentioned in the sectional descriptions) and as the genus includes many important weeds its seed characters have been well-documented, e.g. by Gunn (1970). In spite of this, their variation has not contributed much to the infrageneric classification of the genus. Two main features are useful in this context.

Hilum length. The length of the hilum in *Vicia* varies from $\frac{1}{16}$ to $\frac{3}{4}$ of the circumference of the seeds. A survey shows that, in general, perennials have long hila while annuals have short ones. There are some exceptional annuals with long hila (e.g. *V. grandiflora*, *V. reverchonii*), but no perennials with hila less than $\frac{1}{8}$ of the seed's circumference. (The same relationship pertains in *Lathyrus*.) Since annuals are believed to be evolved from perennials, this suggests that the long hilum is relatively primitive in the Vicieae. Paradoxically, however, short hila are predominant in the Papilionoideae as a whole and are apparently primitive within the subfamily.

Lens position. The 'lens' is a small circular thickening of the testa on the trajectory of the vascular bundle (Corner, 1951); its function is unknown. In

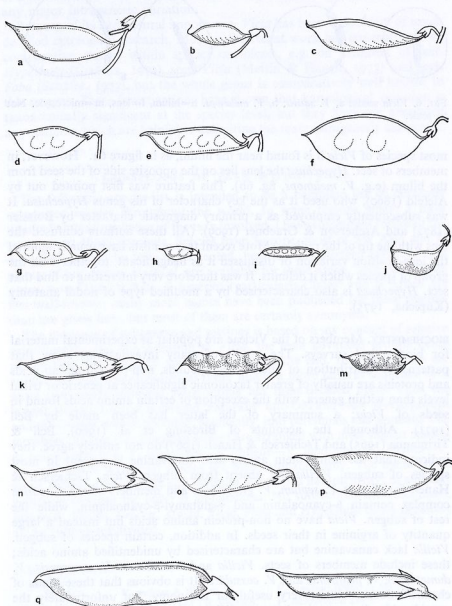


FIG. 5. *Vicia* fruits: a, *V. crocea*; b, *V. cassubica*; c, *V. cracca*; d, *V. disperma*; e, *V. leucantha*; f, *V. durandii*; g, *V. vicioides*; h, *V. hirsuta*; i, *V. pubescens*; j, *V. lunata*; k, *V. cappadocica*; l, *V. ervilia*; m, *V. caesarea*; n, *V. oroboides*; o, *V. hyrcanica*; p, *V. michauxii*; q, *V. narbonensis*; r, *V. sativa*. All natural size.

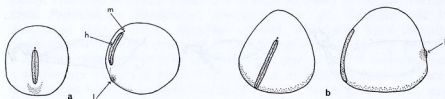


FIG. 6. *Vicia* seeds: a, *V. sativa*; b, *V. melanops*. h=hilum, l=lens, m=micropyle. Not to scale.

most species of *Vicia* it is found near the hilum, as in figure 6a. However, in members of sect. *Hypechusa* the lens lies on the opposite side of the seed from the hilum (e.g. *V. melanops*, fig. 6b). This feature was first pointed out by Alefeld (1860), who used it as the key character of his genus *Hypechusa*. It was subsequently employed as a primary diagnostic character by Boissier (1872) and Ascherson & Graebner (1909). (All these authors confused the lens with the tip of the radicle.) More recent taxonomists have usually ignored the lens-position variation or dismissed it as insignificant, together with the group of species which it delimits. It was therefore very interesting to find that sect. *Hypechusa* is also characterised by a modified type of nodal anatomy (Kupicha, 1975).

BIOCHEMISTRY. Members of the Viciae are popular as experimental material for biochemical surveys. The results of many investigations show that patterns of distribution of phenolic compounds, non-protein amino acids and proteins are usually of greater taxonomic significance at generic or tribal levels than within genera, with the exception of certain amino acids found in seeds of *Vicia*; a summary of the latter has been made by Bell (1971). Although the accounts of Birdsong et al. (1960), Bell & Tirimanna (1965) and Tschiersch & Hanelt (1967) do not entirely agree, they indicate that the non-protein amino acid canavanine is present in most species of subgen. *Vicilla* but absent from subgen. *Vicia*. Tschiersch & Hanelt found that *V. sepium*, *V. grandiflora* and members of the *V. sativa* complex contain β -cyanoalanin and γ -glutamyl- β -cyanoalanin, while the rest of subgen. *Vicia* have no non-protein amino acids but instead a large quantity of arginine in their seeds. In addition, certain species of subgen. *Vicilla* lack canavanine but are characterised by unidentified amino acids; these include members of sects. *Vicilla* and *Cassubicae*: *V. amurensis*, *V. dumetorum*, *V. pisiformis* and *V. cassubica*. It is obvious that these kinds of chemical data could be very useful for taxonomy, but unfortunately the considerable discrepancies between different workers' results prevent the distribution patterns disclosed so far being used with complete confidence.

MINOR VARIABLE CHARACTERS. The leaves of *Vicia* vary in number and shape of leaflets, density of indumentum, presence or absence of tendrils and shape of stipules; these different states often provide useful 'spot' characters but in general are not significant at sectional level. The flowers vary in colour and size in a similar manner, as do the number of seeds per fruit. The pollen of

Vicia has not been fully surveyed, but a sample of 11 species, made as part of a wider study in the Viciae (Clarke & Kupicha, in press) has not revealed any major intrageneric variation.

Because of its agricultural importance, *Vicia* has been the subject of much detailed cytological research. Most of the recent work has concentrated on comparative studies within species complexes, e.g. on members of sect. *Hypechusa* (Činčura, 1970), sect. *Vicia* (Metten & Hanelt, 1973) and sect. *Faba* (Schäfer, 1973), but the whole genus is comparatively well known in this respect. These investigations have shown that karyological variation is taxonomically significant at the species level, but they have not generated any patterns which are helpful in delimiting the main infrageneric categories.

CONSPECTUS OF TAXA WITHIN VICIA

The following species-list is intended to be a complete list of currently recognised species throughout the world. In some regions where I have relatively little knowledge of the taxa involved, I have sometimes followed the most recent Flora accounts. Species from Europe, most of SW Asia and N America* should be fully documented, because fine modern revisions and plenty of herbarium material are available for these areas. Members of the genus from C and E Asia, S America (particularly Chile)* and N Africa are less well-known; many more names have been published for these regions than are given here, but most of them are certainly synonyms.

The sequence of subgenera and sections is based on my concept of relative primitiveness and specialisation in *Vicia*, the least advanced groups being placed first and the most specialised towards the end. In each section the species are listed in alphabetical order unless a more natural sequence or a more convenient informal subgrouping has been decided upon. Thus the largest section, *Cracca*, is divided 'naturally' into Old and New World groups and the former then subdivided 'artificially' into perennials and annuals. The members of these two Eurasian groups are arranged with most similar species as neighbours (e.g. *V. ciceroidea*—*V. rafigae*—*V. multijuga*; *V. hirsuta*—*V. terroni*); the N American species are listed alphabetically. The members of sects. *Vicilla*, *Atossa*, *Vicia* and *Faba* are placed in a natural array; in all other polytypic sections the order is alphabetical. No subsections are recognised, but sects. *Vicilla*, *Cracca*, *Atossa*, *Vicia*, *Faba* and *Hypechusa* could probably all be further subdivided.

I. Subgenus VICILLA

sections:

1. *Vicilla*

<i>V. unijuga</i> A. Braun	<i>V. venulosa</i> Boiss. & Hohen.
<i>V. crocea</i> (Desf.) B. Fedtsch.	<i>V. dichroantha</i> Diels
<i>V. venosa</i> (Willd.) Maxim.	<i>V. amoena</i> Fischer
<i>V. nipponica</i> Matsum.	<i>V. amurensis</i> Oettel
<i>V. kulingiana</i> L. H. Bailey	<i>V. japonica</i> A. Gray
<i>V. pseudo-orobus</i> Fischer & C. A. Meyer	<i>V. pisiformis</i> L.
<i>V. hirticalycina</i> Nakai	<i>V. sylvatica</i> L.
	<i>V. dumetorum</i> L.

* The N American species of *Vicia* have been revised by Hermann (1960), and those of Argentina by Burkart (1966).

2. *Cassubicae*

<i>V. abbreviata</i> Fischer	<i>V. multicaulis</i> Ledeb.
ex Sprengel	<i>V. nigricans</i> Hook. & Arn.
<i>V. cassubica</i> L.	<i>V. orobus</i> DC.
<i>V. dadianorum</i> Sommier & Levier	<i>V. semiglabra</i> Rupr. ex Boiss.
<i>V. montenegrina</i> Rohl.	<i>V. sparsiflora</i> Ten.
3. *Perditae*

<i>V. dennesiana</i> H. C. Watson	
-----------------------------------	--
4. *Cracca*

Old World members—perennials	
<i>V. cracca</i> L. agg.	<i>V. glareosa</i> P. H. Davis
<i>V. pinetorum</i> Boiss. & Spruner	<i>V. sicula</i> (Raf.) Guss.
<i>V. sibthorpii</i> Boiss.	<i>V. alpestris</i> Steven
<i>V. ochroleuca</i> Ten.	<i>V. ciceroidea</i> Boiss.
<i>V. atlantica</i> Pomel	<i>V. rafgae</i> Tamamschian
<i>V. splendens</i> P. H. Davis	<i>V. multijuga</i> (Boiss.) Rech. f.
<i>V. kotschyana</i> Boiss.	<i>V. glauca</i> C. Presl
Old World members—annuals	
<i>V. villosa</i> Roth agg.	<i>V. palaestina</i> Boiss.
<i>V. benghalensis</i> L.	<i>V. hulensis</i> Plitm.
<i>V. scandens</i> R. P. Murray	<i>V. disperma</i> DC.
<i>V. cirrhosa</i> Webb & Berthel.	<i>V. durandii</i> Boiss.
<i>V. chaetocalyx</i> Webb & Berthel.	<i>V. vicioides</i> (Desf.) Cout.
<i>V. filicaulis</i> Webb & Berthel.	<i>V. hirsuta</i> (L.) Gray
<i>V. monantha</i> Retz.	<i>V. terronii</i> (Ten.) Lindb. f.
<i>V. leucantha</i> Biv.	
New World members	
<i>V. acutifolia</i> Elliott	<i>V. ludoviciana</i> Nutt.
<i>V. caroliniana</i> Walter	<i>V. mexicana</i> Hemsley
<i>V. exigua</i> Nutt.	<i>V. minutiflora</i> Dietr.
<i>V. floridana</i> S. Watson	<i>V. pulchella</i> Kunth
<i>V. hugeri</i> Small	<i>V. reverchonii</i> S. Watson
<i>V. leavenworthii</i> Torrey & A. Gray	
5. *Variegatae*

<i>V. argentea</i> Lapeyr.	<i>V. megalotropis</i> Ledeb.
<i>V. canescens</i> Labill. agg.	
6. *Pedunculatae*

<i>V. altissima</i> Desf.	<i>V. onobrychioides</i> L.
<i>V. cedretorum</i> Font Quer	
7. *Americanae*

<i>V. americana</i> Mühl. ex Willd.	
-------------------------------------	--
8. *Subvillosae*

<i>V. subvillosa</i> (Ledeb.) Trautv.	
---------------------------------------	--
9. *Volutae*

<i>V. biennis</i> L.	
----------------------	--
10. *Panduratae*

<i>V. cappadocica</i> Boiss. & Bal.	<i>V. cretica</i> Boiss. & Heldr.
<i>V. cassia</i> Boiss.	
11. *Ervum*

<i>V. laxiflora</i> Brot.	<i>V. tetrasperma</i> (L.) Schreber
<i>V. pubescens</i> (DC.) Link	
12. *Ervoides*

<i>V. articulata</i> Hornem.	
------------------------------	--
13. *Ervilia*

<i>V. ervilia</i> (L.) Willd.	
-------------------------------	--
14. *Lentopsis*

<i>V. caesarea</i> Boiss. & Bal.	
----------------------------------	--

- | | | |
|---------------------------|---|--|
| 15. <i>Trigonellopsis</i> | <i>V. cypria</i> Kotschy ex Unger
& Kotschy
<i>V. lunata</i> (Boiss. & Bal.) Boiss. | <i>V. singarensis</i> Boiss. & Hausskn. |
| 16. <i>Australes</i> | <i>V. andicola</i> Kunth
<i>V. bijuga</i> Gillies ex Hook.
<i>V. petiolaris</i> Burkart
<i>V. graminea</i> Smith
<i>V. linearifolia</i> Hook. & Arn.
<i>V. macrograminea</i> Burkart | <i>V. montevidensis</i> Vogel
<i>V. nana</i> Vogel
<i>V. pampicola</i> Burkart
<i>V. peruviana</i> Vilchez
<i>V. platensis</i> Speg.
<i>V. setifolia</i> Kunth
<i>V. stenophylla</i> Vogel |
| 17. <i>Mediocinetæ</i> | <i>V. leucophaea</i> Greene | |
- II. Subgenus *VICIA*
- | | | |
|-----------------------|---|--|
| 18. <i>Atossa</i> | <i>V. oroboides</i> Wulfen
<i>V. sepium</i> L. | <i>V. balansae</i> Boiss.
<i>V. truncatula</i> Fischer ex M. Bieb. |
| 19. <i>Vicia</i> | <i>V. pyrenaica</i> Pourret
<i>V. sativa</i> L. agg.
<i>V. grandiflora</i> Scop. | <i>V. barbazitæ</i> Ten. & Guss.
<i>V. lathyroides</i> L.
<i>V. cuspidata</i> Boiss. |
| 20. <i>Faba</i> | <i>V. faba</i> L.
<i>V. narbonensis</i> L.
<i>V. galilæa</i> Plitm. & Zohary | <i>V. haeniscyamus</i> Mouterde
<i>V. johannis</i> Tamamschian
<i>V. bithynica</i> (L.) L. |
| 21. <i>Hypechusa</i> | <i>V. anatolica</i> Turrill
<i>V. assyriaca</i> Boiss.
<i>V. ciliatula</i> Lipsky
<i>V. esdraelonensis</i> O. Warb.
& Eig
<i>V. galeata</i> Boiss.
<i>V. hybrida</i> L. | <i>V. hyrcanica</i> Fischer & C. A. Meyer
<i>V. lutea</i> L.
<i>V. melanops</i> Sibth. & Smith
<i>V. noeana</i> Reuter ex Boiss.
<i>V. pannonica</i> Crantz
<i>V. sericocarpa</i> Fenzl |
| 22. <i>Peregrinae</i> | <i>V. aintabensis</i> Boiss. & Hausskn.
<i>V. michauxii</i> Sprengel | <i>V. mollis</i> Boiss. & Hausskn. ex Boiss.
<i>V. peregrina</i> L. |

Other species. *V. quadrijuga* P. H. Davis is an annual known only from the type gathering, which was collected in NE Anatolia. The leaves are mucronate, with few pairs of leaflets; the inflorescence 1-2-flowered; and the flowers pale yellow, with irregular calyx, ovate standard and dorsally compressed, evenly pubescent style. Davis & Plitmann (1970) suggest that *V. quadrijuga* is allied to *V. ervilia*, and its vegetative and floral characters support this idea. The delimitation of the small 'ervoid' sections of *Vicia* is particularly critical, and depends largely on legume characters. Since the mature legume of *V. quadrijuga* is unknown, it seems best to delay making a firm decision about its taxonomic relationships until this evidence is available.

KEY TO THE SUBGENERA AND SECTIONS OF *VICIA*

- | | |
|---|---|
| 1. Stipules with nectariferous spot on abaxial surface; inflorescence much shorter than the subtending leaf, usually 1-few-flowered [subgen. <i>Vicia</i>] | 2 |
| + Stipules without nectariferous spot; inflorescence usually equaling or exceeding the subtending leaf, usually many-flowered [subgen. <i>Vicilla</i>] | 7 |

2. Calyx subregular; sutures of legume parallel 3
- + Calyx irregular; sutures of legume not parallel 4
3. Leaves usually with more than three pairs of leaflets (if fewer, then leaflets less than 1 cm long); lateral veins of leaflets prominent and straight sect. 19. *Vicia*
- + Leaves with 1-3 pairs of leaflets which are more than 2 cm long; lateral veins of leaflets not prominent, curving towards apex sect. 20. *Faba*
4. Inflorescence several-flowered; vexillum oblong 5
- + Inflorescence 1-2-flowered; vexillum stenonychioid (i.e. with banner wider than claw) 6
5. Perennial; lens of seed close to hilum sect. 18. *Atossa*
- + Annual; lens of seed opposite hilum sect. 21. *Hypechusa*
6. Flowers yellow or white; lens of seed opposite hilum sect. 21. *Hypechusa*
- + Flowers purplish; lens of seed close to hilum sect. 22. *Peregrinae*
7. Vexillum oblong 8
- + Vexillum platonychioid, stenonychioid or ovate 11
8. Perennials with many-flowered inflorescences; if stipules dimorphic, neither of the pair lacinate 9
- + Annual, with few-flowered inflorescences; stipules strongly dimorphic, one of the pair finely lacinate sect. 12. *Ervoidea*
9. Leaves hypostomatic, usually with few pairs of leaflets sect. 1. *Vicilla*
- + Leaves epistomatic, usually with many pairs of leaflets 10
10. Style dorsally compressed sect. 2. *Cassubicae*
- + Style laterally compressed sect. 3. *Perditae*
11. Vexillum platonychioid (i.e. pandurate, 'waisted') 12
- + Vexillum stenonychioid to ovate 14
12. Style laterally compressed sect. 4. *Cracca*
- + Style dorsally compressed 13
13. Perennials; style glabrous adaxially, densely bearded on abaxial side sect. 5. *Variegatae*
- + Annuals; style pubescent all round, tufted on abaxial side sect. 10. *Panduratae*
14. Perennials 15
- + Annuals 21
15. Style terete, bearing a dense ring of hairs clearly separated from the stigma sect. 17. *Mediocinctae*
- + Style dorsally compressed, pubescent near the stigma 16
16. Leaves imparipinnate sect. 8. *Subvillosae*
- + Leaves tendrillous or mucronate 17
17. Style tufted abaxially 18
- + Style evenly pubescent all round 20
18. Flowers 1 cm or less in length; plants of S America sect. 16. *Australes*
- + Flowers 1.5 cm or more in length; plants of N America or the Old World 19

19. Vexillum stenonychioid; plants of the W Mediterranean sect. 6. *Pedunculatae*
 + Vexillum oblong; plants of N America sect. 7. *Americanae*
 20. Vernation of leaflets conduplicate; stipules conspicuously dentate
 (*V. sylvatica*) sect. 1. *Vicilla*
 + Vernation of leaflets supervolute; stipules semi-sagittate or
 lanceolate, entire sect. 9. *Volutae*
 21. Style tufted abaxially; plants of S America sect. 16. *Australiae*
 + Style not as above; plants of Eurasia 22
 22. Leaflets with supervolute vernation; plants up to 1.5 m, with
 5-15-flowered racemes sect. 9. *Volutae*
 + Leaflets with conduplicate vernation; plants seldom exceeding
 0.5 m, with few-flowered racemes 23
 23. Legumes subtorulose 24
 + Legumes not subtorulose 25
 24. Seeds subglobose; calyx teeth equal; leaves mucronate
 sect. 13. *Ervilia*
 + Seeds lenticular; upper calyx teeth longer than lowermost one;
 leaves with a simple tendril sect. 14. *Lentopsis*
 25. Leaves with 2-4 pairs of linear leaflets; style c. 1 mm long,
 bearing a few minute hairs sect. 11. *Ervum*
 + Leaves with 4 or more pairs of ovate leaflets; style c. 5 mm long,
 evenly and fairly densely pubescent sect. 15. *Trigonellopsis*

SUBGENERIC AND SECTIONAL DESCRIPTIONS

I. Subgenus *Vicilla* (Schur) Rouy in Rouy & Fouc., Fl. Fr. 5:205 (1899).

Syn.: *Vicilla* Schur, Enum. Pl. Transs. 170 (1866); *Vicia* subgen. *Cracca* (Dum.) Gams in Hegi, Ill. Fl. Mitteleur. 43:1499 (1924).

Plants perennial or annual. Stems always with complete replacement of cortical vascular bundles at the nodes. Leaves hypostomatic to epistomatic, paripinnate and tendrillous or mucronate or rarely imparipinnate; stipules very occasionally dimorphic, never with nectariferous glands. Inflorescence 1-many-flowered, usually equalling or longer than subtending leaf. Calyx teeth equal or unequal. Vexillum oblong, stenonychioid or platonychioid, always glabrous. Style rarely terete, usually dorsally or laterally compressed, the pubescence even all round, tufted abaxially or rarely in dorsiventral or lateral patches. Legume often \pm stipitate, not containing 'woolly' parenchyma; sutures of fruit rarely parallel. Seeds with long to short hilum; testa smooth; lens always near hilum; canavanine usually present.

Lectotype (Gunn, 1969): *V. pisiformis* L., Sp. Pl. 734 (1753).

1. Sect. *Vicilla* (Schur) Aschers. & Graebner, Syn. Mitteleur. Fl. 6,2:916 (1909).

Syn.: *Vicilla* Schur, Enum. Pl. Transs. 170 (1866); *Swantia* Alef. in Oesterr. Bot. Z. 9:365 (1859); *Vicia* sect. *Crocea* Radzhi in Novit. Syst. Pl. Vasc. (Leningrad) 7:230 (1971).

Plants perennial. Leaves hypostomatic, hypo-amphistomatic or rarely (in *V. sylvatica*) epi-amphistomatic, tendrillous or mucronate, usually with few

pairs of large, broad leaflets; stipules rarely dimorphic (in *V. crocea*). Inflorescence many-flowered, sometimes a panicle; pedicels often subtended by bracteoles. Flowers deep orange-yellow or pale yellow, whitish or purple. Calyx irregular; vexillum oblong; style dorsally compressed or rarely terete, evenly hairy all round or rarely tufted abaxially. Legume stipitate. Seeds with medium to long hilum.—c. 15 species.

Lectotype (Gunn, 1969): *V. pisiformis* L., Sp. Pl. 734 (1753).

Europe (except S Iberian peninsula, Turkey-in-Europe & some Mediterranean islands), N Anatolia, Crimea, Caucasia, N Iran, Asia eastwards to Japan.

The genus *Vicilla* Schur arose originally as a development of Godron's treatment of *Vicia* s.l. Godron (1848) had redefined *Vicia* to include only large-flowered species with dorsally compressed styles; he excluded *Cracca* and *Ervum* as separate genera. In 1866 Schur circumscribed *Vicia* even more narrowly so that it comprised only species whose styles are tufted abaxially; species in which the styles are hairy all round were placed in *Vicilla*. This genus included *V. pisiformis*, *V. sylvatica*, *V. cassubica* and *V. orobus*. Ascherson & Graebner (1909) later used *Vicilla* as a section within 'sect.' *Cracca* (see note on p. 288), but they widened its definition to include some tufted-styled species (*V. dumetorum* and *V. altissima*) as well as adding to it a new taxon from Asia (*V. unijuga*). Since then there have been few attempts to subdivide *Vicia*, most Flora writers being content to treat sect. (or subgen.) *Cracca* as if it were a homogenous group. Radzhi (1971) has recently engaged in this task, though he deals only with Caucasian species. He classifies subgen. *Cracca* into four sections, dividing the species which I include in sect. *Vicilla* between two of them: *V. crocea* forms a monotypic section, while *V. cassubica*, *V. pisiformis* and *V. biennis* comprise sect. *Cassubicae* Radzhi. These two sections are differentiated by the style being terete in *V. crocea* but dorsally compressed in the other species, and also by the relative lengths of keel and standard.

The lectotype of *Vicilla* Schur is *V. pisiformis*, and, as my first section is defined primarily on the original 'key' character of this genus (style dorsally compressed, evenly hairy all round), it is reasonable to use Schur's name for it. The concept of *Vicilla* is considerably changed, however. The group contains only species with hypostomatic leaves, and hence *V. cassubica* and *V. orobus* are removed to another section. The members of sect. *Vicilla* have more or less oblong vexilla and do not, therefore, include *V. altissima* or *V. onobrychioides*; the exclusion of these two species is further supported by their styles being tufted abaxially. I consider, however, that *V. dumetorum* should be placed within sect. *Vicilla* despite its tufted style, on the grounds that its leaves are strongly hypostomatic, the leaflets relatively broad, and the vexillum oblong.

Sect. *Vicilla* includes a number of species very similar in facies to members of *Lathyrus* sect. *Orobus* (L.) Gren. & Godron *sensu* Bässler, 1973.* These

* The members of *Lathyrus* concerned can be distinguished from *Vicia* by four 'key' features: their leaflets have supervolute, not conduplicate, vernation; the staminal tube is truncate at the apex, not oblique; the style is pubescent only on the adaxial (inner) surface; the fruits are not stipitate.

are woodland plants with a predominantly eastern north temperate distribution. The most 'extreme' examples of the facies, *V. venosa*, *V. crocea*, *V. unijuga* and *V. kulingiana*, have tendrillous leaves with very large, broad, papery-coriaceous, reticulate-veined leaflets. The inflorescence is paniculate, its lateral branches subtended by bracts and the pedicels by bracteoles. Other species of sect. *Vicilla* possess characteristics linking them with more typical members of *Vicia*. *V. pseudo-orobus* has smaller, more numerous leaflets, and tendrils; *V. pisiformis* also has tendrils and the leaflets, though large and broad, are more herbaceous in texture than those of *V. unijuga*. *V. sylvatica* has multijugate, epi-amphistomatic leaves with small leaflets; the flowers are fewer than in the 'oroboid' species and are borne in a loose raceme; and the vexillum is intermediate between oblong and stenonychioid.

2. Sect. *Cassubicae* Radzhi in Novit. Syst. Pl. Vasc. (Leningrad) 7:230 (1971). Syn.: *Vicilla* Schur, Enum. Pl. Transs. 170 (1866), pro parte excl. typ.

Plants perennial. Leaves epistomatic, tendrillous or mucronate or sometimes imparipinnate; leaflets numerous, ovate. Inflorescence many-flowered, racemose, ebracteolate. Flowers yellow, whitish, pink or purple. Calyx irregular; vexillum oblong; style dorsally compressed, evenly pubescent all round. Seeds with hilum of long to medium length.—c. 9 species.

Type: *V. cassubica* L., Sp. Pl. 735 (1753).

Europe except some Mediterranean islands, N Anatolia, Lebanon, N Iran, Caucasia, Crimea, Asia eastwards to Japan; W coast of N America; Chile.

In its original form, sect. *Cassubicae* Radzhi had virtually the same delimitation as the genus *Vicilla*, but with *V. cassubica* as its type. *V. cassubica* belongs to an assemblage of closely allied species with a distinctive facies: their leaves, like those of the 'oroboid' group, are often tendrillous and membranous, but the leaflets are smaller and more numerous. Moreover, in strong contrast to members of sect. *Vicilla*, these species have epistomatic leaves. The floral characters of these sections are very similar, and the two groups are probably quite closely related.

Sect. *Cassubicae* is predominantly an Old World group, but it contains one American species, *V. nigricans* (syn. *V. gigantea* Hook.). The latter is quite distinct from all other New World natives of *Vicia*: it is very much larger; it is the only species with a dorsally compressed and evenly hairy style; the leaves are epistomatic; it is the only member of the genus found in both N and S America.

V. nigricans has well-developed tendrils, but among the other members of the section there is a strong tendency towards reduction to mucronate leaves. *V. abbreviata*, and some plants of *V. semiglabra*, are unusual in having leaves with a terminal leaflet; this trait is found otherwise only in *V. subvillosa* and *V. argentea* (sects. *Subvillosae* and *Variiegatae*, respectively).

3. Sect. *Perditae* Kupicha, sect. nov.

Plantae robustae, perennes, caulibus repentibus. Folia stomatibus solus supra, multijuga, cirrhosa, foliolis oblongis. Inflorescentia multiflora, dense ramosa, ebracteolata. Flores fusco-flavescentes. Calyx inordinatus; vexillum oblongum; stylus lateraliter compressus, omnino pubescens. Semina ignota.

Plants stout, perennial, with creeping branches. Leaves epistomatic,

tendrillous; leaflets numerous, oblong. Inflorescence many-flowered, densely racemose, ebracteolate. Flowers brownish-yellow. Calyx irregular; vexillum oblong; style laterally compressed, evenly pubescent all round. Seeds unknown.—Monotypic.

Type: *V. dennesiana* H. C. Watson in Godman, Nat. Hist. Azores 155 (1870). Azores (now extinct ?).

In general habit, leaf-shape, stomatal distribution and vexillum shape *V. dennesiana* is similar to members of sect. *Cassubicae*, while its laterally compressed style suggests a relationship with sect. *Cracca*. It is interesting that both these groups have an amphi-Atlantic distribution, while *V. dennesiana* occurred on the Azores, in mid-Atlantic. Is it a vain hope that this beautiful species might be rediscovered?

4. Sect. *Cracca* Dumort., Fl. Belg. 103 (1827).

Syn.: *Cracca* Medik. in Vorles. Churpf. Phys. Ges. 2:359 (1787), non L. (1753); *Vicia* a. *Cracca* Gray, Nat. Arr. Brit. Pl. 2:614 (1821); *Cracca* sect. *Ervoidea* Godron in Gren. & Godron, Fl. Fr. 1:471 (1848), pro parte excl. typ.; *Endiusa* Alef. in Oesterr. Bot. Z. 9:359 (1859); *Vicia* subgen. *Pseudervoidea* Rouy in Rouy & Fouc., Fl. Fr. 5:232 (1899); *Vicia* sect. *Lenticula* Aschers. & Graebner, Syn. Mitteleur. Fl. 6,2:905 (1909).

Plants perennial or annual. Leaves amphistomatic to epistomatic, usually tendrillous, multijugate. Inflorescence racemose, many- to few-flowered. Flowers large and brightly coloured (yellowish, crimson and purple) to small and pale. Calyx irregular, often gibbous at the base; vexillum platonychoid; style laterally compressed, \pm evenly pubescent all round, sometimes somewhat tufted abaxially or with indumentum in dorsiventral patches. Seeds with long to short hilum.—c. 40 species.

Type: *V. cracca* L., Sp. Pl. 735 (1753).

Europe, N Africa, Canaries, Azores, SW Asia, Crimea, Caucasia, Transcaspia, Asia eastwards to Japan, N America.

Section *Cracca* is the largest and most variable taxon of this rank within *Vicia*. The 'core' of the section, as delimited here, includes those species which Godron (1848) placed in the illegitimate genus *Cracca*, whose key character was the laterally compressed style. Since that time, however, the assemblage of species which possess this feature has rarely been recognised as a unit. Two trends have brought this about: first, the tendency of taxonomists to group together all members of *Vicia* which have small, pale flowers; second, the decreasing interest which more modern authors have shown in the fine morphological details which their predecessors often recorded so carefully.

'*Cracca*' is reinstated here with confidence that it is a natural group. This is due mainly to the discovery that, except in sect. *Perditae*, the laterally compressed style is always accompanied by a platonychoid vexillum, while this form of standard is rare outside the group. The delimitation of sect. *Cracca* by these two characters involves the disruption of some other generally recognised groups within *Vicia*, notably '*Ervum*'. In its narrowest definition, *Ervum* L. in the sense of Godron (1848) contained only *V. tetrasperma*,

V. pubescens and *V. laxiflora*; in its broadest* sense, 'sect.' *Ervum sensu* Ascherson & Graebner also included *V. ervilia*, *V. hirsuta*, *V. articulata* and *V. monantha*. Recent authors, e.g. Ball (1968) and Davis & Plitmann (1970), have tended to take a wide view of this group. I consider that this modern treatment is artificial and unnatural; the ervoid species share certain general features but in detail they form a heterogeneous collection. This is illustrated not only by their floral structures but by the striking differences in their fruits. Several species which Ball places in sect. *Ervum*, viz. *V. leucantha*, *V. vicioides*, *V. durandii*, *V. disperma* and *V. filicaulis* (syn. *V. bifoliolata* Rodr.), have laterally compressed styles, pandurate vexilla and stipitate pods, and are therefore transferred to sect. *Cracca*. This applies also to *V. monantha*, which Ascherson & Graebner put in 'sect.' *Ervum*. Other ervoid species, e.g. *V. tetrasperma*, *V. ervilia* and *V. articulata*, are excluded from sect. *Cracca* because they have ovate or oblong standards, dorsally compressed styles and non-stipitate fruits of a variety of characteristic shapes. *V. hirsuta* and *V. terronii* (syn. *V. meyeri* Boiss.) are moved to sect. *Cracca*, but by association with other species rather than by their own possession of the sectional characters. Their flowers are so small and simple (due, presumably, to the evolution of a predominantly autogamous breeding-system) that the form of their parts cannot be used as taxonomic evidence; the style is reduced to a minute, terete, few-haired process, while the standard is ovate. They are, however, very similar in other respects to the slightly more robust *V. palaestina*, which has the style and standard typical of sect. *Cracca*.

A correlation between laterally compressed styles and platonychoid vexilla is found again in most N American representatives of *Vicia*. In other characteristics (leaf shape, stomatal distribution, shape of fruits, etc.) these species agree well with Old World members of sect. *Cracca* and are therefore united with them.

Within sect. *Cracca* there is a wide range of morphological variation. The majority of species have multijugate, tendrillous leaves and dense, many-flowered racemes, but there are several exceptions to this generalisation. For example, *V. sicula* has etendrillous leaves and its leaflets are few, very long and coriaceous, and have inrolled margins. *V. filicaulis* is few-flowered, and the whole plant is modified to produce an extremely slender climber with narrow leaflets and long, delicate, branched tendrils. The closely related species *V. ciceroidea*, *V. rafigae* and *V. multijuga* are xerophytes with coriaceous leaflets and hard, circinnate or almost spinous tendrils. The style in these three is distinctive in being hairy only on the adaxial and abaxial edges, not on the sides.

5. Sect. *Variegatae* Radzhi in Novit. Syst. Pl. Vasc. (Leningrad) 7:230 (1971).

Plants perennial. Leaves amphistomatic to epistomatic, multijugate, often with dense indumentum; tendrils often reduced or absent; leaves sometimes imparipinnate. Inflorescence many-flowered. Flowers white to purplish. Calyx irregular; vexillum platonychoid; style dorsally compressed, densely bearded on the abaxial side. Seeds with hilum of medium length.—3 species.

* Alefeld (1859) had a concept of *Ervum* totally out of line with all other authors: in his sense the genus *Ervum* contained perennials, e.g. *V. unijuga*, as well as small-flowered annuals.

Type: *V. variegata* Willd., Sp. Pl. 3:1096 (1802) [*V. canescens* Labill. subsp. *variegata* (Willd.) P. H. Davis in Davis, Fl. Turkey 3:287 (1970)].

Pyrenees, S Italy, S Inner and NE Anatolia, Caucasias, N Iran, W Syria, C Asia.

The members of sect. *Variegatae* form an easily-recognised group whose superficial unity is confirmed by other more cryptic features. Radzhi (1971) was probably the first to describe accurately the style of these species; it is of a type unique to the section, being strongly dorsally compressed, glabrous on the inner surface and long-bearded abaxially. I have shown, moreover, that in sect. *Variegatae* the vexillum is of the platynychioid type, which occurs otherwise only in sects. *Cracca* and *Panduratae*. Members of sect. *Variegatae*, like those of sects. *Vicilla* and *Cassubicae*, show a tendency towards reduction of the tendrils. Some members of the polytypic *V. canescens* have mucronate leaves, while in most plants of *V. argentea* they are imparipinnate.

Sect. *Variegatae* is a disjunct group of alpine species. Its members are found in the Pyrenees (*V. argentea*), S Italy, Anatolia and Caucasias (*V. canescens* s.l.) and C Asia (*V. megalotropis*).

6. Sect. *Pedunculatae* Rouy in Rouy & Fouc., Fl. Fr. 5:221 (1899).

Plants perennial. Leaves epi-amphistomatic, multijugate and tendrillous, with linear leaflets. Inflorescence a loose raceme of several relatively large flowers. Flowers whitish, yellow or purple. Calyx irregular; vexillum stenonychioid; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with short to long hilum.—3 species.

Lectotype designated here: *V. onobrychioides* L., Sp. Pl. 735 (1753).

S Europe excluding Turkey-in-Europe, NW Africa.

V. onobrychioides, *V. altissima* and *V. dumetorum* have the same type of style as members of subgen. *Vicia*, and were placed together with these species by some early taxonomists (e.g. Godron, 1848; Rouy, 1899). Later authors tended to overlook this character in favour of the stronger phenetic similarity between *V. onobrychioides* etc. and members of subgen. *Vicilla* (then usually known as sect. *Cracca*). The oblong vexillum and hypostomatic leaves of *V. dumetorum* show a strong enough link with members of sect. *Vicilla* to justify its inclusion there. *V. onobrychioides* and *V. altissima*, on the other hand, have standards with a broad banner, the leaves are epi-amphistomatic, and the leaflets are linear rather than ovate. It seems probable that these two taxa are quite closely related to members of sect. *Vicilla*, but have diverged from them following two recognisable trends: towards a more xerophytic habitat, and towards a condition where the individual flower, rather than the inflorescence, has become the attractive unit.

V. cedretorum, endemic to the Rif region of Morocco, is very similar in habit to the other two members of sect. *Pedunculatae*, and it has the same distinctive kind of style. The vexillum is not as pronouncedly stenonychioid, however, the banner being only a little wider than the claw. Despite this, it seems certain that the three species comprise a natural group within *Vicia*.

7. Sect. *Americanae* Kupicha, sect. nov.

Syn.: *Abacosa* Alef. in Bonplandia 9:102 (1861).

Plantae perennes. *Folia* stomatibus adaxialibus plus quam abaxialibus, multijuga, cirrhosa. *Inflorescentia* 5-7-flora. *Flores* comparate grandes (c. 1.5 cm longi), purpurascens, in racemos laxos dispositi. *Calyx* inordinatus; vexillum oblongum; stylus dorsaliter compressus, omnino pubescens sed abaxialiter barbatus. *Semina* hilo longo.

Plants perennial. Leaves epi-amphistomatic, multijugate, tendrillous. Inflorescence several-flowered; flowers comparatively large and borne in a loose raceme, purplish. Calyx irregular; vexillum oblong; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with long hilum.—Monotypic.

Type: *V. americana* Mühl. ex Willd., Sp. Pl. 3:1096 (1802).

N America excluding the SE states, China.

V. americana is an extremely polymorphic species (Gunn, 1968), but despite its internal diversity it seems to be taxonomically isolated, at least in the New World. It is quite distinct from the N American members of sect. *Cracca*, and also from *V. nigricans*. The species which are most alike in morphology belong to the small W Mediterranean sect. *Pedunculatae*, but I hesitate to unite *V. americana* with this section without further study; it would be surprising if such a disjunct group proved to be natural. Sects. *Pedunculatae* and *Americanae* can, however, be distinguished only by the different shapes of their vexilla, which are stenonychioid and oblong, respectively. In stylar characters, *V. americana* resembles the S American species of *Vicia*. It is possible that this fact holds a clue to the origin of sect. *Australiae*, but at present there are few other indications linking the two groups.

V. americana also occurs in E Asia, but is represented here only by var. *tridentata* (Gunn, op. cit.). The centre of variability of this species is N American, and its extension into China, though not necessarily due to man, may be relatively recent in evolutionary terms.

8. Sect. *Subvillosae* Kupicha, sect. nov.

Plantae perennes. *Folia* stomatibus in superficiebus ambabus pariter dispositis, imparipinnata, paucifoliolata; foliola subulata, villosa. *Inflorescentia* pauciflora (floribus 2-4). *Flores* magni, purpurascens. *Calyx* subregularis; vexillum obovato-spathulatum; stylus dorsaliter compressus, adaxialiter abaxialiterque pubescens.

Plants perennial. Leaves amphistomatic, imparipinnate; leaflets few per leaf, subulate, villous. Inflorescence of few, large, purple flowers. Calyx subregular; vexillum stenonychioid; style dorsally compressed, pubescent on adaxial and abaxial faces.—Monotypic.

Type: *V. subvillosa* (Ledeb.) Trautv. in Acta Horti Petrop. 3:42 (1875). [Syn.:

Orobis subvillosus Ledeb., Fl. Alt. 3:359 (1831).]

Afghanistan north-east to Tien Shan.

V. subvillosa is a particularly beautiful and interesting species. Like members of sect. *Variegatae*, it inhabits screes at high altitudes and has leaves which are densely hairy and tendrillous; as in members of sect.

Pedunculatae, the flowers are large and attractive and the vexillum is stenonychioid. It possesses several individual characters: the leaves have a terminal leaflet, the calyx is subregular and the style has a unique pattern of indumentum-distribution (fig. 4e).

It is interesting to compare *V. subvillosa* with other groups in the tribe Viciae which share a similarly rocky, alpine habitat: for example, *Vicia* sect. *Variegatae*, *Lathyrus* sect. *Lathyrostylis* (Griseb.) Bässler and the ditypic genus *Vavilovia* Fedorov. All show a tendency towards loss of tendrils, and it seems reasonable to infer that during the evolution of these comparatively specialised perennials, this morphological effect may have arisen repeatedly and independently in response to similar environmental conditions.

9. Sect. *Volutae* Kupicha, sect. nov.

Plantae annuae vel biennes. *Folia* stomatibus adaxialibus plus quam abaxialibus, multijuga, cirrhosa; foliola linearia, vernatione supervolutiva. *Inflorescentia* densa, multiflora. *Flores* violacei. *Calyx* inordinatus; vexillum obovato-spathulatum; stylus dorsaliter compressus, aequaliter omnino pubescens. *Semina* hilo medio longo.

Plants annual or biennial. Leaves epi-amphistomatic, multijugate, tendrillous; leaflets linear, with supervolute vernation. Inflorescence dense, many-flowered. Flowers violet. Calyx irregular; standard stenonychioid; style dorsally compressed, evenly hairy all round. Seeds with hilum of medium length.—Monotypic.

Type: *V. biennis* L., Sp. Pl. 736 (1753).

SE Europe, S Russia, Caucasia.

Although in facies closely similar to some members of sect. *Cracca*, *V. biennis* possesses several characters which argue against such an association. Its flower differs from those of sect. *Cracca* in having a stenonychioid standard and a dorsally compressed style; it is distinguished from those of sect. *Pedunculatae* in having the style not tufted but evenly pubescent all round. *V. biennis* is unique within *Vicia* in having its leaflets curled, rather than folded, in bud; this feature is otherwise confined to the genera *Lathyrus* and *Vavilovia*. In other respects *V. biennis* is a typical member of *Vicia*, and its anomalous vernation is perhaps not necessarily an indication of close phylogenetic relationship with either of these other genera; the character may have arisen as an independent mutation.

10. Sect. *Panduratae* Kupicha, sect. nov.

Plantae annuae. *Folia* stomatibus adaxialibus plus quam abaxialibus, cirrhosa, pauci- vel plurijuga; foliola linearia. *Inflorescentia* 1-12-flora. *Flores* purpurei vel violacei. *Calyx* inordinatus gibbosusque aut subregularis; vexillum panduratum; stylus dorsaliter compressus, omnino pubescens sed abaxialiter barbatus. *Semina* hilo brevi.

Annuals. Leaves epi-amphistomatic, tendrillous; leaflets few- to several-paired, linear. Inflorescence 1-few-flowered. Flowers reddish-purple to violet. Calyx irregular and gibbous or subregular; standard platonychioid; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with short hilum.—3 species.

Type: *V. cappadocica* Boiss. & Bal. in Boiss., Diagn. ser. 2, 6:68 (1859).
Greece, Cyprus, S & Inner Anatolia, W Syria, N & NW Iran, Transcaucasia.

The members of this group are very similar in general appearance to some of the more delicate representatives of sect. *Cracca* (e.g. *V. monantha*, *V. glauca*, *V. leucantha*). This impression is supported by the pandurate vexilla found in all members of sect. *Panduratae* and by the gibbous calyces of *V. cassia* and *V. cretica*. The only conflicting characters lie in the gynoeceum: instead of being laterally compressed and evenly hairy all round, the styles in sect. *Panduratae* are dorsally flattened and tufted on the outer face.

As Table 2 shows, this type of style occurs in many species of *Vicia*, not all of which are closely related. It is typical of subgen. *Vicia*, and this is one of the reasons why Radzhi (1971) places *V. cappadocica* with *V. sativa* and *V. bithynica* in sect. *Vicia*. The subregular calyx and linear, non-stipitate fruits of *V. cappadocica* provide further evidence to support this arrangement. Equally strong arguments, however, can be used against it: *V. cappadocica* does not have stipular nectaries, the peduncle is long and the standard is pandurate. Due to this balance of conflicting factors, *V. cappadocica* has given taxonomists considerable trouble in the past. Because it has leaves with few pairs of leaflets, it has also sometimes been placed in *Lathyrus*, as *L. trijugus* Bornm. or *L. ptucijugus* (Trautv.) Schischkin.

The distribution of the dorsally compressed, tufted style within *Vicia* is of particular interest. It occurs without exception in the well-defined subgen. *Vicia* and sporadically outside it: in S American species (except *V. nigricans*), in the N American *V. americana*, in *V. dumetorum* and in sects. *Pedunculatae* and *Panduratae*. The constancy of the trait in some cases (within subgen. *Vicia* and on the S American continent) suggests that it has special taxonomic and functional significance there, and so its occasional appearance in other places is given equally strong weighting. The justification of this depends on how easily and how often this type of style can evolve. Its distribution pattern, which is disjunct both geographically and taxonomically, suggests that it has a polyphyletic origin within *Vicia*, and although it is difficult to envisage how such a distinctive form could have arisen more than once, it seems likely that this has been the case. Perhaps the abaxially tufted style has an advantage over the evenly hairy style in promoting cross-pollination, and is a specialisation in the evolution of the floral mechanism. One can deduce, from its occurrence throughout the whole of subgen. *Vicia*, that the tufted style is not a recent feature but was present at early stages in the evolution of *Vicia*. In the light of these considerations it seems justified to use such styler characters to provide guides for the division, if not the unification, of taxa.

11. Sect. *Ervum* (L.) Taub. in Engl. & Prantl, Nat. Pflanzenfam. 3, iii:350 (1894).

Syn.: *Ervum* L., Sp. Pl. 738 (1753); *Vicia* subgen. *Ervum* (L.) Rouy in Rouy & Fouc., Fl. Fr. 5:245 (1899).

Plants annual. Leaves amphi- to epistomatic, tendrillous, with few pairs of small, elliptical leaflets. Inflorescence few-flowered. Flowers small and pale. Calyx subregular; vexillum oblong to ovate; style terete to (slightly) dorsally compressed, sparsely hairy all round. Fruits less than 2 cm long, not stipitate, linear. Seeds with short hilum.—3 species.

Lectotype (Hitchcock & Green, 1929): *V. tetrasperma* (L.) Schreber, Spicil. Fl. Lips. 26 (1771).

Europe, N Africa, Palestine, W Syria, N Iraq, outer Anatolia, Crimea, Caucasia, Asia eastwards to China.

The classification of ervoid members of *Vicia* was mentioned earlier under sect. 4 *Cracca*. The species which are here included in sect. *Ervum* represent the core of closely allied taxa related to *V. tetrasperma*, the lectotype of the genus *Ervum* L. This narrow view coincides with the concept of Godron (1848), but conflicts with the opinions of the majority of more modern authors. The species which comprise sect. *Ervum* are united by their fruit type: the legume is very small (less than 2 cm long), not stipitate, and has parallel sutures (fig. 5i).

The ervoid species will always present a problem, because their flowers are simple (probably reduced or degenerate through adaptation to autogamy) and the usual taxonomic guides—standard shape and styler details—are more or less obliterated. However, although it may not be possible to link members of the ervoid group with other sections of *Vicia*, this assemblage should not be treated as a 'dustbin' section but should rather be subdivided into smaller groups (even if these are rather inconvenient) whose internal affinity is certain. These can then be regarded as 'natural' taxa of equal status within the hierarchy, and further phylogenetic speculation about their mutual relationship need not disturb the classification. Sects. *Ervoidea*, *Ervilia* and *Lentopsis* are all of this type, having been segregated from the nebulous ervoid group.

12. Sect. *Ervoidea* (Godron) Kupicha, **comb. nov.**

Syn.: *Coppoleria* Todaro in Atti Accad. Sci. Litt. Palermo ser. 2, 1:14 (1845); *Cracca* Medik. sect. *Ervoidea* Godron in Gren. & Godron, Fl. Fr. 1:471 (1848); *Parallosa* Alef. in Oesterr. Bot. Z. 9:359 (1859); *Vicia* subgen. *Ervoidea* (Godron) Rouy in Rouy & Fouc., Fl. Fr. 5:241 (1899).

Plants annual. Leaves epi-amphistomatic, multijugate, tendrillous, with narrow leaflets; stipules dimorphic: one simple, the other finely laciniate. Inflorescence 1–2-flowered. Flowers lilac. Calyx slightly irregular; vexillum oblong; style dorsally compressed, evenly pubescent all round. Legume subtorulose. Seeds with short hilum.—Monotypic.

Lectotype designated here: *V. articulata* Hornem., Enum. Pl. Hort. Haun. 41 (1807).

Italy, Balkans, Corsica, Sardinia, Sicily, Crete, W Turkey.

V. articulata has long alternated in position between the two broad groups 'Cracca' and 'Ervum', without having obvious strong affinities with any other species. It is isolated by two striking morphological features: it has subtorulose fruits, and dimorphic stipules in which one of the pair is simple, the other composed of many fine radiating branches. In its fruit *V. articulata* approaches *V. ervilia* and *V. caesarea*; in the laciniate stipules, *V. singarensis* and *Anatropostylia* (*Vicia*) *koeieana*. The floral characters, however, provide taxonomic evidence of a different persuasion: the standard is oblong, and the style dorsally compressed (not laterally, cf. Townsend, 1974) and evenly

pubescent as in the perennial (more primitive?) sections *Vicilla* and *Cassubicae*. On balance it seems best to separate *V. articulata* as a monotypic section.

The genus *Cracca* sensu Godron (1848) contained members of the *Vicia*-affinity with laterally compressed styles; species with brightly coloured, many-flowered inflorescences were placed in sect. *Eucracca*, and those with small, pale flowers in sect. *Ervoides*. The latter contained several species which are here classified in sect. *Cracca* (*V. hirsuta*, *V. disperma* and *V. monantha*), and *V. articulata*. *V. articulata* is chosen as the lectotype of sect. *Ervoides*, despite its possession of a dorsally compressed style, in order to avoid introducing more new names into the classification of *Vicia*.

13. Sect. *Ervilia* (Link) W. Koch, Syn. Fl. Germ. ed. 1:191 (1836).

Syn.: *Ervilia* Link, Enum. Hort. Berol. 2:240 (1822). *Ervum* sect. *Ervilia* (Link) Ser. in DC., Prodr. 2:366 (1825); *Vicia* subgen. *Ervilia* (Link) Rouy in Rouy & Fouc., Fl. Fr. 5:248 (1899).

Plants annual. Leaves epi-amphistomatic, multijugate, mucronate; leaflets linear. Inflorescence with one to several small pale-lilac flowers. Calyx subregular with equal teeth; vexillum ovate; style dorsally compressed, varying from pubescent all round to only on adaxial face. Fruits subtorulose. Seeds with short hilum.—Monotypic.

Type: *V. ervilia* (L.) Willd., Sp. Pl. 3:1103 (1802).

S Europe, N Africa, Palestine, W Syria, N Iraq, W Iran, W & S Anatolia.

The isolated position of *V. ervilia* has been recognised almost since the beginning of classification of *Vicia*. It was segregated as a monotypic genus by Link (1822) and by Godron (1848), while in Taubert's scheme (1894) this taxon had the rank of a section within *Vicia*. Other authors have taken a wider view of sect. *Ervilia*. In the sense of Seringe (1825) it included *V. tetrasperma* and *V. articulata* as well as the type species. Lastly, Plittmann (1967) has used *Ervilia* as a series, comprising *V. ervilia* and *V. caesarea*, within sect. *Ervum*.

V. ervilia was placed within the ervoid assemblage because it has small, pale flowers in sparse racemes. It differs from other members in having a bushy habit; tendrils are absent and the plant does not support itself on neighbouring vegetation. In addition, the leaves have very many leaflets (8–20 pairs), the fruit is subtorulose and the style is sometimes hairy only on the inner side. *V. ervilia* is often cultivated as a fodder crop in Mediterranean countries and it is possible that some of its characteristics (e.g. the tendrillous leaves) have been selected by man.

14. Sect. *Lentopsis* Kupicha, sect. nov.

Plantae annuae. Folia stomatibus in superficiebus ambabus pariter dispositis, cirrhosa, pauci- vel plurijuga; folia parva, elliptica. Inflorescentia pauciflora. Flores bicolores, lavandulacei albidique. Calyx subregularis, dentibus superis quam infero longioribus; vexillum obovatum, saccis parvis duobus; stylus dorsaliter compressus, omnino pubescens. Legumen subtorulosus. Semina lentiformia, hilo brevi.

Plants annual. Leaves amphistomatic, tendrillous, with few to several pairs of small elliptic leaflets. Inflorescence few-flowered. Flowers bicoloured lavender-blue and white. Calyx subregular, with upper teeth longer than the lowest one; vexillum ovate, with two small pouches; style dorsally compressed, pubescent all round. Fruit subtorulose. Seeds lenticular, with short hilum.—Monotypic.

Type: *V. caesarea* Boiss. & Bal. in Boiss., Diagn. ser. 2, 6:69 (1859).

C and adjacent S Anatolia.

Since it is endemic to Turkey, *V. caesarea* has rarely been considered in relation to the rest of *Vicia* and has had an uneventful taxonomic history. The synonymous *V. vulcanica* Hand.-Mazz. was described under the mistaken impression that it was perennial. Plitmann (1967) places *V. caesarea* in ser. *Ervilia*, within sect. *Ervum*; it is linked with *V. ervilia* because both have subtorulose legumes. In other characters, however, *V. caesarea* appears to be quite distinct from *V. ervilia* (i.e. in the presence of tendrils; the shape of calyx and standard; the style type; and in the lenticular seeds), and I do not consider that the evidence justifies such a close association of the two species. In habit, *V. caesarea* is remarkably similar to *Lens*, and certain details of its morphology (the bossed standard and flattened seeds) support this superficial resemblance.

15. Sect. *Trigonellopsis* Rech. fil. in Ark. Bot. 5:260 (1959).

Syn.: *Sellunia* Alef. in Oesterr. Bot. Z. 9:358 (1859).

Plants annual. Leaves epistomatic, multijugate, tendrillous, with broadly elliptic leaflets. Inflorescence few-flowered. Flowers pale yellow or bicoloured, bluish and yellowish. Calyx subregular; standard stenonychioid; style long and slender, dorsally compressed, evenly hairy all round. Fruits sometimes (i.e. in *V. lunata*) somewhat inflated, with papery, indehiscent valves. Seeds with short hilum, lenticular in *V. lunata*.—3 species.

Type: *V. lunata* (Boiss. & Bal.) Boiss., Fl. Or. 2:594 (1872).

Cyprus, W & S Anatolia, W Syria, N Iraq.

Sect. *Trigonellopsis* was originally monotypic and based on *V. lunata*. This species is distinct from all others in having broadly crescentic fruits whose valves become papery and somewhat inflated on maturity (fig. 5j). *V. cypria* and *V. singarensis* have legumes of a more usual form, but share with *V. lunata* several features which confirm their close relationship. The leaflets in all three are rather distantly placed on the rachis and are broadly elliptic to emarginate or praemorse. The stipules in *V. lunata* and *V. cypria* are sometimes fringed with slender laciniae, and those of *V. singarensis* are deeply divided into fimbriate segments like the stipules of *V. articulata* and *Anatropostylia koeieana*. The flowers of *V. lunata* and *V. cypria* are alike in general appearance and detail. The vexilla are large and blue, forming a contrast with the yellow wings and keel. The standards are stenonychioid, while the styles are distinctively long and slender. The flowers of *V. singarensis* are similar in shape but uniformly pale blue.

16. Sect. Australes Kupicha, sect. nov.

Plantae annuae et perennes, graciles. *Folia* stomatibus adaxialibus plus quam abaxialibus, cirrhosa, plerumque paucijuga. *Inflorescentia* pauci- vel multiflora. *Flores* albi ad lazulinos. *Calyx* subregularis vel inordinatus; vexillum obovato-spatulatum vel oblongum; stylus dorsaliter compressus, omnino pubescens sed abaxialiter barbatus. *Semina* hilo longo vel brevi.

Slender annuals and perennials. Leaves epi-amphistomatic, tendrillous, usually with few pairs of leaflets. Inflorescence few- to many-flowered. Flowers white to deep blue. Calyx subregular to irregular; vexillum stenonychioid to oblong; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with long to short hilum.—c. 13 species.

Type: *V. graminea* Smith in Rees, Cyclop. 37, no. 27 (1817).

Mexico, Colombia, Peru; S America south of lat. 25°S.

Apart from *V. nigricans*, the S American members of *Vicia* form a closely-related complex of species whose boundaries are often difficult to determine and may possibly be affected by hybridisation. Although their styler characters suggest an affinity with subgen. *Vicia*, there is no other really convincing evidence for this; stipular nectaries are absent and the inflorescence is usually borne on a long peduncle (*V. bijuga* and *V. linearifolia* are unusual in having sessile flowers). In habit *V. graminea* s.l. is reminiscent of the W Mediterranean *V. filicaulis*, but floral details show that the former is not a member of sect. *Cracca*. I agree with Hanelt & Mettin (1970) that the affinities of S American species of *Vicia* lie more with subgen. *Vicilla* than with subgen. *Vicia*, and consider them sufficiently distinct, as a group, to merit classification in an independent section.

17. Sect. Mediocinctae Kupicha, sect. nov.

Plantae perennes. *Folia* stomatibus adaxialibus plus quam abaxialibus, cirrhosa, paucijuga. *Inflorescentia* 1-2-flora. *Flores* lutescentes. *Calyx* subregularis; vexillum obovato-spatulatum; stylus teres, arcuatus, ad medium annulo pilorum cinctus. *Semina* hilo medio longo.

Plants perennial. Leaves epi-amphistomatic, tendrillous, with few pairs of leaflets. Inflorescence 1-few-flowered. Flowers yellowish. Calyx subregular; vexillum stenonychioid; style terete, arcuate, with a dense ring of hairs at some distance from the stigma. Seeds with hilum of medium length.—Monotypic.

Type: *V. leucophaea* Greene in Bot. Gaz. 6:217 (1881).

New Mexico.

In habit, *V. leucophaea* (syn. *V. mediocincta* S. Watson) resembles the N American members of sect. *Cracca*, but it differs from them in floral details. The standard is stenonychioid rather than pandurate, and the style has a form unique within the genus (fig. 4h). *V. leucophaea* could be compared with *V. subvillosa*: both are taxonomically isolated perennials inhabiting restricted mountainous localities; both have villous leaves and few-flowered racemes in which the individual blooms are conspicuous.

II. Subgenus *Vicia*

Plants perennial or annual. Stems sometimes with partial replacement of cortical vascular bundles at nodes. Leaves hypostomatic to hypo-amphistomatic, paripinnate, usually tendrillous, occasionally mucronate; stipules monomorphic, always with a glandular nectariferous pit on the abaxial side. Inflorescence 1-several-flowered, always shorter than the subtending leaf; flowers sometimes sessile in leaf axil. Calyx regular or irregular. Vexillum oblong or stenonychioid, rarely pubescent on the adaxial side. Style dorsally compressed, hairy all round or only on abaxial side, always tufted abaxially. Legume not stipitate, containing \pm well-developed 'woolly' parenchymatous tissue between the seeds; pods rhomboidal or linear. Seeds with long to short hila; testa smooth or rarely rough; lens near hilum or on opposite side of the seed; canavanine absent.

Type: *V. sativa* L., Sp. Pl. 736 (1753).

18. Sect. *Atossa* (Alef.) Aschers. & Graebner, Syn. Mitteleur. Fl. 6,2:949 (1909).

Syn.: *Orobus* L., Sp. Pl. 728 (1753), pro parte excl. typ.; *Vicioides* Moench, Meth. 135 (1794); *Atossa* Alef. in Bonplandia 9:100 (1861); *Vicia* sect. *Pedunculatae* Rouy in Rouy & Fouc., Fl. Fr. 5:221 (1899) pro parte excl. typ.; *Vicia* sect. *Sepium* Radzhi in Novit. Syst. Pl. Vasc. (Leningrad) 7:235 (1971).

Plants perennial. Stems with complete replacement of cortical vascular bundles at nodes. Leaves hypostomatic, tendrillous or mucronate; leaflets few-several-paired. Inflorescence pedunculate, several-flowered. Flowers pale yellow or bluish-purple. Calyx irregular; vexillum oblong, glabrous. Legume with sutures somewhat curved, not parallel. Seeds with hilum encircling over half the circumference; lens near hilum; testa smooth.—4 species.

Lectotype (Gunn, 1969): *V. sepium* L., Sp. Pl. 737 (1753).

Europe except Sardinia and Turkey-in-Europe, N Anatolia, Crimea, Caucasus, N Iran, Asia eastwards to the Pacific.

The species of this small and rather heterogeneous group inhabit deciduous woods or hedgerows, and share with other more distantly related members of the tribe several characteristics which appear to be associated with a mesophytic habitat. Thus, although *V. sepium* has a scrambling habit, the others tend to grow erect and free from supporting vegetation, *V. truncatula* and *V. oroboides* having etendrillous leaves. Members of the section all have strongly hypostomatic leaves; this trait, among others, serves to distinguish *V. truncatula* and *V. balansae* from the species of sect. *Cassubicae* (e.g. *V. orobus*, *V. cassubica*) which are very similar in habit. Like many woodland species, members of sect. *Atossa* have dense inflorescences which are conspicuous in number of flowers rather than by the attractiveness of each bloom. The flowers themselves do not have broad banners as in the majority of the subgenus, but oblong vexilla (fig. 3i). Finally, the long hila of the seeds of sect. *Atossa* are also typical of other perennials in *Vicia* and *Lathyrus*.

V. oroboides was originally classified by Linnaeus as a member of the genus *Orobus* (*O. lathyroides*); it is remarkable for its resemblance to members of *Lathyrus* sect. *Orobus* and 'oroboid' species of *Vicia* sect. *Vicilla* (see p. 308). I agree with Bässler (1973) that the facies of this phenetic assemblage has probably evolved separately several times, in response to similar environmental conditions; there is no doubt that *V. oroboides* is a true member of subgen. *Vicia* since it possesses all the key characters of this well-defined group.

19. Sect. *Vicia*

Syn.: *Cujunia* Alef. in Bonplandia 9:101 (1861); *Vicia* sect. *Subsessiles* Rouy in Rouy & Fouc., Fl. Fr. 5:208 (1899).

Plants annual or perennial. Stems with complete replacement of cortical vascular bundles at the nodes. Leaves hypo-amphistomatic, tendrillous; leaflets several- to many-paired. Inflorescence 1-2-flowered; flowers sessile in the leaf axils, pale yellow, purple or lavender. Calyx teeth equal; vexillum stenonychioid, glabrous. Legume with parallel sutures. Seeds with hilum very long to very short; lens near hilum; testa rough or smooth.—c. 6 species.

Type: *V. sativa* L., Sp. Pl. 736 (1753).

Europe, N Africa, SW Asia, Crimea, Caucasus, Transcaucasia, Asia eastwards to Japan.

Sect. *Vicia* comprises an undoubtedly natural group of species and yet contains a fairly wide range of character-variation. On one hand there is the only perennial species, *V. pyrenaica*, endemic to the Sierra Nevada and the Pyrenees; on the other, the polymorphic cosmopolitan weed *V. sativa*, the type of the genus, which some authors divide into five or more microspecies or subspecies (cf. Mettin, 1958; Mettin & Hanelt, 1964; Hanelt & Mettin, 1966; Ball, 1968).

Members of this section can often be recognised by their foliage: the leaflets, although variable in dimensions, are usually emarginate and mucronate, and have prominent, straight lateral veins. *V. grandiflora* has seeds in which the hilum occupies over half the circumference; in Old World species of *Vicia* this trait is otherwise confined to perennials (as in sect. *Atossa*), but it is common in American species, including the annuals. Ascherson & Graebner (1909) attempted to divide 'sect.' *Euicia* (equivalent to subgen. *Vicia*) into two groups based on hilum length; in their arrangement *V. grandiflora* was placed with *V. sepium*. However, apart from its anomalous seeds, *V. grandiflora* is a typical member of sect. *Vicia*. The two small species *V. lathyroides* and *V. cuspidata* are unusual within the genus in having rough-coated seeds; they can be differentiated by the patterning on the testa surface.

The present taxonomic arrangement is not supported by the distribution of free amino acids found in some members of the subgenus. Seeds of *V. sativa*, *V. grandiflora* and *V. sepium* were reported by Tschiersch & Hanelt (1967) to contain the poisonous (lathyrogenic) substances β -cyanoalanin and γ -glutamyl- β -cyanoalanin, but this was absent from *V. lathyroides*. The latter and all other species of subgen. *Vicia* tested had relatively large quantities of arginine in their seeds instead. Unfortunately *V. oroboides*, *V. truncatula* and *V. balansaе* were not screened for this character, so it is not possible to assess the full implications of its distribution pattern.

20. Sect. *Faba* (Miller) Ledeb., Fl. Ross. 1:664 (1842).

Syn.: *Faba* Miller, Gard. Dict. ed. 4 (1754); *Arachus* Medik. in Vorles. Churpf. Phys. Ges. 2:360 (1787); *Vicia* sect. *Arachus* (Medik.) Tutin in Clapham, Tutin & Warburg, Fl. Brit. Is. 447 (1952).

Plants annual. Stems with complete replacement of cortical vascular bundles at nodes. Leaves hypo-amphistomatic, tendrillous or mucronate, with few (1-3) pairs of large leaflets. Inflorescence 1-2-flowered; flowers pedunculate or sessile in the leaf-axils, whitish or purple. Calyx regular; vexillum stenonychioid, glabrous. Legume with parallel sutures. Seeds with short hilum; lens near hilum; testa smooth.—6 species.

Type: *V. faba* L., Sp. Pl. 737 (1753).

W & S Europe, N Africa, Palestine, W Syria, Syrian Desert, N Iraq, W Iran, S Anatolia, Crimea.

V. faba itself occurs only in cultivation, or as an escape, but although its precise origins are unknown there are closely similar wild relatives (*V. narbonensis* and the recently described *V. haeniscyamus* and *V. galilaea*). The characters which are associated with its role as a crop plant (absence of tendrils, stout habit, very large leaves) have been heavily weighted in the past; Fedtschenko (1948) even made *V. faba* the basis of a monotypic subgenus equivalent in status to the rest of the genus! *V. faba* and *V. narbonensis* are in most respects typical members of subgen. *Vicia*, and their possession of all its key-characters is surely of much greater significance, in the construction of a natural classification, than features which were probably selected by man.

V. bithynica has only recently been associated with the *V. faba* group; it is a distinctive species with an unsettled taxonomic history. In habit *V. bithynica* stands apart from the other members of sect. *Faba*; it is more slender and has well-developed tendrils, and the flowers are often borne on a long peduncle and pedicel. However, the characters which it shares with them suggest that sect. *Faba*, as defined here, is probably a natural group. In its regular calyx, parallel-sided pods and dentate stipules, sect. *Faba* appears to have some affinity with sect. *Vicia*.

21. Sect. *Hypechusa* (Alef.) Aschers. & Graebner, Syn. Mitteleur. Fl. 6,2:957 (1909).

Syn.: *Hypechusa* Alef. in Bot. Zeitung (Berlin) 18:165 (1860); *Vicia* sect. *Subsessiles* Rouy in Rouy & Fouc., Fl. Fr. 5:208 (1899), pro parte excl. typ.; *Vicia* sect. *Pedunculatae* Rouy, op. cit. 221, pro parte excl. typ.

Plants annual. Stems with partial replacement of cortical vascular bundles at the nodes. Leaves epi- or hypo-amphistomatic, tendrillous; leaflets many-paired. Inflorescence 1-many-flowered. Flowers pedunculate or sessile in the leaf-axils, yellowish or rarely purplish. Calyx irregular; vexillum oblong or stenonychioid, occasionally pubescent on inner side. Legume rhomboidal (sutures not parallel). Seeds with medium to short hilum; lens on opposite side of the seed from the hilum; testa smooth.—12 species.

Lectotype (Gunn, 1969): *V. lutea* L., Sp. Pl. 736 (1753).

W, S & C Europe, Crimea, N Africa, SW Asia, Caucasias, Transcaspia.

This group was first distinguished by Alefeld (1860) as a genus of the subtribe *Viciosae* (equivalent to the subgen. *Vicia*); it was based on the lens position, on flower colour, and on the absence of spongy tissue within the legume (but see below). Boissier (1872) was the only taxonomist to follow Alefeld in recognising this assemblage as a unit; Ascherson & Graebner also made use of the lens-position character, but in conjunction with the non-correlated variation in hilum length, and the delimitation of '*Hypechusa*' was consequently altered. Recent authors have usually ignored variation in lens position in *Vicia*. For example, Plitmann (1967) divides the species of sect. *Hypechusa* between four groups without suggesting that these possess a sign of close relationship within the hierarchy. *Hypechusa* is reinstated here as a section chiefly because of the discovery of another character confined to this group—a variation in nodal anatomy. Its members appear to be unique within the tribe in that the replacement of cortical vascular bundles at the nodes of the mature plant is partial rather than complete (Kupicha, 1975).

This section comprises some very attractive plants and considerable morphological variation. Most of the species have sessile flowers, solitary or twinned in the leaf-axils, and the vexilla in these flowers have a wide banner and narrow claw (e.g. *V. galeata*, fig. 3k). A few species, however, have several-flowered inflorescences on short peduncles (e.g. *V. pannonica* and *V. melanops*), and in these the vexillum is oblong. These characteristics belong to a syndrome which is generally typical of perennial woodland species of the tribe; their presence here in weedy annuals is therefore particularly interesting and suggests that these species are relatively primitive within sect. *Hypechusa*.

Other distinctive characters which occur within the section may be mentioned: *V. pannonica*, *V. hybrida* and *V. anatolica* are unique within the tribe in having pubescent standards; *V. lutea* has pods bearing long tuberculate-based hairs; and *V. melanops* has curiously-coloured flowers in which the wings are greenish yellow with a conspicuous velvety black spot. Alefeld considered that the fruits of sect. *Hypechusa* do not contain spongy tissue, but this distinction cannot be supported. All members of subgen. *Vicia* seem to have 'woolly' mesophyll within their legumes, but in some species it is more strongly developed than in others.

22. Sect. *Peregrinae* Kupicha, sect. nov.

Syn.: *Tuamina* Alef. in Bonplandia 9:102 (1861); *Vicia* sect. *Subsessiles* Rouy in Rouy & Fouc., Fl. Fr. 5:208 (1899), pro parte excl. typ.

Plantae annuae. *Caules* ad nodos substitutione tota fascium vascularium corticalium. *Folia* stomatibus adaxialibus paulo plus quam abaxialibus, cirrhosa, multijuga. *Inflorescentia* uniflora, non pedunculata sed floribus in pedicellis satis longis portatis. *Flores* albidi, flavescentes vel atrovioleacei. *Calyx* inordinatus; vexillum obovato-spathulatum. *Legumen* rhombeum, suturis non parallelis. *Semina* hilo brevissimo; lens prope hilum; testa rasilis.

Plants annual. Stems with complete replacement of cortical vascular bundles at the nodes. Leaves weakly epi-amphistomatic, tendrillous, multi-jugate. Inflorescence 1-flowered, not pedunculate but flowers borne on fairly

long pedicels. Flowers whitish, pale yellow or dark violet. Calyx irregular; vexillum stenonychioid, glabrous. Legume rhomboidal (sutures not parallel). Seeds with very short hila; lens near hilum; testa smooth.—4 species.

Type: *V. peregrina* L., Sp. Pl. 737 (1753).

S Europe, N Africa, Crimea, SW Asia eastwards to Afghanistan.

This section is based on a group delimited by Boissier (1872). Its species are not morphologically striking, but form a convenient assemblage which is probably also a natural one. Members of sect. *Peregrinae* often have very narrow leaflets. Their flowers are characteristically not completely sessile but are borne on short pedicels; the peduncle is absent. *V. michauxii* is unusual within the genus (excepting sect. *Faba*) in having large seeds which are up to 1 cm long.

ACKNOWLEDGMENTS

This paper presents part of the work carried out for the degree of Ph.D. in the University of Edinburgh. I thank the Science Research Council and the Senatus Academicus of Edinburgh University for their generous financial support, and Professor R. Brown and the Regius Keeper of the Edinburgh Royal Botanic Garden for their permission to work in the University Botany Department and at the Garden, respectively. I am most grateful to my two supervisors, Dr P. H. Davis and Dr P. M. Smith, for their interest, encouragement and helpful advice.

REFERENCES

- ALEFELD, F. (1859). Ueber die Vicieen. *Oesterr. Bot. Z.* 9:352–366.
 — (1860). Hypechusa, nov. gen. Viciarum. *Bot. Zeitung (Berlin)* 18:165–166.
 — (1861). Ueber Vicieen. *Bonplandia* 9:66–72, 99–105.
 ASCHERSON, P. F. A. & GRAEBNER, C. O. R. P. P. (1909). Vicia in *Synopsis der mitteleuropäischen Flora* 6,2:902–995. Leipzig.
 BALL, P. W. (1968). Vicia in Tutin, T. G. et al. (ed.), *Flora Europaea* 2:129–136. Cambridge U.P.
 BÄSSLER, M. (1966). Die Stellung des Subgen. *Orobis* (L.) Baker in der Gattung *Lathyrus* L. und seine systematische Gliederung. *Feddes Repert.* 72:69–97.
 — (1973). Revision der eurasiatischen Arten von *Lathyrus* L. Sect. *Orobis* (L.) Gren. & Godr. *Feddes Repert.* 84:329–447.
 BELL, E. A. (1971). Comparative biochemistry of non-protein amino acids, in Harborne, J. B., Boulter, D. & Turner, B.L. (eds), *Chemotaxonomy of the Leguminosae* 179–206. Academic Press.
 BELL, E. A. & TIRIMANNA, A. S. L. (1965). Associations of amino acids and related compounds in the seeds of 47 species of Vicia: their taxonomic and nutritional significance. *Biochem. J.* 97:104–111.
 BIRDSONG, B. A., ALSTON, R. & TURNER, B. L. (1960). Distribution of canavanine in the family Leguminosae as related to phyletic groupings. *Canad. J. Bot.* 38:499–505.
 BOISSIER, E. (1872). Vicia and Ervum in *Flora Orientalis* 2:565–599. Geneva & Basel.
 BURKART, A. (1966). Notas sobre las Especies argentinas de Vicia (Leguminosae) del área mesopotámico-pampeana. *Darwiniana* 14,1:161–193.

- ČINČURA, F. (1970). Bemerkungen zur Zytotaxonomie einiger fremdländischer Arten der Gattung *Vicia* L. (Wicke). *Acta F.R.N. Univ. Comen. Bot.* 18:17-35.
- CLARKE, G. C. S. & KUPICHA, F. K. (in press). The relationships of the genus *Cicer* L. (Leguminosae): the evidence from pollen morphology. *J. Linn. Soc., Bot.*
- CORNER, E. J. H. (1951). The leguminous seed. *Phytomorphology* 1:117-150.
- DAVIS, P. H. (1970). *Flora of Turkey and the East Aegean Islands* 3. Edinburgh U.P.
- & PLITTMANN, U. (1970). *Vicia* in Davis, P. H. (ed.), *Flora of Turkey and the East Aegean Islands* 3:274-325. Edinburgh U.P.
- FEDTSCHENKO, B. A. (1948). *Vicia* in Komarov, V. L., *Flora URSS* 13:406-475. Moscow & Leningrad.
- GAMS, H. (1924). *Vicia* in Hegi, G., *Illustrierte Flora von Mittel-Europa* 4,3:1506-1562. München.
- GODRON, D. A. (1848). *Vicia*, *Ervum* & *Ervilia* in Grenier, J. C. M. & Godron, *Flore de France* 1:458-475. Paris & Besançon.
- GUINEA, L. E. (1953). *Estudio de las Vezas y Arvejas españolas (Monografía del Genero Vicia)*. Instituto Nacional de Investigaciones Agronomicas, Madrid.
- GUNN, C. R. (1968). The *Vicia* americana complex (Leguminosae). *Iowa State Coll. J. Sci.* 42,3:171-214.
- (1969). Genera, types and lectotypes in the tribe Vicieae (Leguminosae). *Taxon* 18:725-733.
- (1970). A key and diagrams for the seeds of 100 species of *Vicia*. *Internat. Seed Testing Assoc. Proc.* 35:773-790.
- HANELT, P. & METTIN, D. (1966). Cytosystematische Untersuchungen in der Artengruppe um *Vicia sativa* L. II. *Kulturpflanze* 14:137-161.
- & METTIN, D. (1970). Ueber die systematische Stellung temperater und meridionaler Sippen der Gattung *Vicia* L. *Feddes Repert.* 81:147-161.
- HERMANN, F. J. (1960). *Vetches of the United States*. U.S.D.A. Agric. Handbk 168. Washington.
- HITCHCOCK, A. S. & GREEN, M. L. (1929). *Int. Bot. Congr. Cambridge (England), 1930, Nom. Prop.* 111-119.
- JANCHEN, E. (1957). *Vicia* in *Catalogus Florae Austriacae* 1,2:375-379.
- KNUTH, P. (1908). *Handbook of flower pollination*. (Based on H. Müller's *The fertilisation of flowers by insects*, translated by J. Ainsworth Davies.) Oxford.
- KUPICHA, F. K. (1973). Studies in the Vicieae I: The new genus *Anatropostylia*. *Notes R.B.G. Edinb.* 32:247-250.
- (1975). Some observations on the vascular anatomy of the Vicieae (Leguminosae). *J. Linn. Soc. Bot.* 70:231-242.
- LINK, J. H. F. (1822). *Vicia* in *Enumeratio plantarum . . . altera* 2:238-240. Berlin.
- MANLEY, R. O. B. (1948). *Bee-keeping in Britain*. Faber & Faber, London.
- METTIN, D. (1958). Zur Morphologie der Chromosomen von *Vicia sativa* L. *Kulturpflanze* 6:116-122.
- & HANELT, P. (1964). Cytosystematische Untersuchungen in der Artengruppe um *Vicia sativa* L. I. *Kulturpflanze* 12:163-225.

- & HANELT, P. (1973). Über Speziationsvorgänge in der Gattung *Vicia* L. *Kulturpflanze* 21:25–54.
- PLITMANN, U. (1967). *Biosystematical study in the annual species of Vicia of the Middle-East*. Hebrew University of Jerusalem.
- PROCTOR, M. & YEO, P. (1973). *The pollination of flowers*. Collins New Naturalist series no. 54.
- RADZHI, A. (1971). Conspectus systematis specierum caucasicarum generis *Vicia* L. *Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR* (Novit. Syst. Pl. Vasc. Leningrad) 7:228–240.
- ROUY, G. C. C. (1899). *Vicia* in Rouy & Foucaud, J., *Flore de France* 5:206–249. Rochelle.
- SALISBURY, E. J. (1928). On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Philos. Trans. Ser. B.* 216:1–65.
- SCHÄFER, H. I. (1973). Zur Taxonomie der *Vicia narbonensis*—Gruppe. *Kulturpflanze* 21:211–273.
- SCHUR, P. J. F. (1866). *Vicia* in *Enumeratio plantarum Transsilvaniae exhibens* 165–171. Vienna.
- SERINGE, N. C. (1825). *Vicia* in De Candolle, A. P., *Prodromus* 2:354–365. Paris.
- SIMOLA, L. K. (1968). Comparative studies on number of leaflets, venation, and epidermal structure in the genus *Lathyrus*. *Canad. J. Bot.* 46:71–84.
- STREICHER, O. (1902). Beiträge zur vergleichenden Anatomie der Viciaceen. *Beih. Bot. Centralbl.* 12:483–538.
- TAUBERT, P. (1894). *Vicia* in Engler & Prantl, *Die natürlichen Pflanzenfamilien* 3,3:350–352. Leipzig.
- TOWNSEND, C. C. (1974). *Vicia* in Townsend & Guest, E. (ed.), *Flora of Iraq* 3:512–544. Baghdad.
- TSCHIRSCH, B. & HANELT, P. (1967). Die freien Aminosäuren der Samen von *Vicia* L. und die systematische Gliederung der Gattung. *Flora*, Abt. A 157:389–406.